The eco-evolutionary dynamics of mutualistic networks: from pattern of emergence to stability

by

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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own original work, that I am the authorship owner thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Signature: H.O. Minoarivelo

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Abstract

The eco-evolutionary dynamics of mutualistic networks: from pattern of emergence to stability

Mutualistic interactions, such as the interactions between flowering plants and their pollinators are ubiquitous in nature. A community in which members are involved in multiple mutualistic interactions forms a mutualistic network. The structure of such a network exhibits well-organized pattern, suggesting that complex ecological and evolutionary processes underlie the assembly of mutualistic networks. Although significant development has recently been achieved in uncovering the structural patterns of mutualistic networks, understanding ecological and evolutionary mechanisms that contribute to the emergence of these patterns and the overall ecological and evolutionary stability of mutualistic communities stays a challenge. Addressing this challenge is the aim of this thesis. We develop a mathematical and simulation model of the ecological dynamics of population densities and the evolutionary dynamics of functional traits of a mutualistic community to deal with the problem. Based on the fact that ecological and evolutionary mechanisms are interdependent, we use the framework of *adaptive dynamics*. We found that the well-organized structural patterns observed in mutualistic networks such as a high nestedness and high modularity can emerge when interactions are trait-dependent and the accessibility to intra and cross trophic resources controlled. Moreover, we found that mutualism plays a determinant role in sustaining evolutionary stability and the productivity of the community. However, the evolutionary trajectories of functional traits in a mutualistic community can experience bistability and bifurcation when mutualistic interactions are highly specialized. In this case, mutualism often creates opportunity empty niche for invasion. Biological invasions targeting a specific peak of empty niche could lead to a strong directional selection in the community. In addition, an introduced species that has a trait different from those of native species and a level of interaction specialization similar to that of the native species is more likely to invade. The structure of the recipient network, such as its nestedness or modularity, is not a primary determinant of invasibility compared to other measurements of network stability such as robustness, resilience and disruptiveness. Consequently, we argue that the interplay of ecological and evolutionary processes through trait-mediated interactions can shed light on important questions in mutualistic networks.

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Opsomming

Die eko-evolusionêre dinamika van mutualistiese netwerke: van patrone van verskyning tot stabiliteit

Mutualistiese interaksies, soos byvoorbeeld die interaksie tussen blomplante en hul bestuiwers, is alomteenwoordig in die natuur. 'n Gemeenskap waarvan die lede aan veelvuldige mutualistiese interaksies deelneem vorm 'n mutualistiese netwerk. Die struktuur van so ŉ netwerk vertoon ŉ goed georganiseerde patroon, wat daarop dui dat komplekse ekologiese en evolusionêre prosesse die samestelling van mutualistiese netwerke aandryf. Hoewel daar onlangs aansienlike vordering gemaak is in die ontdekking van strukturele patrone van mutualistiese netwerke, is dit steeds ŉ uitdaging om die ekologiese en evolusionêre meganismes wat bydra tot hierdie patrone en die algehele stabiliteit van die ekologiese en evolusionêre stabiliteit van mutualistiese gemeenskappe te verstaan. Hierdie uitdaging is dus die doel van hierdie tesis. Om hierdie probleem op te los, ontwikkel ons ŉ wiskundige en simulasie model vir die ekologiese dinamika van populasie digtheid en die evolusionêre dinamika van funksionele eienskappe van ŉ mutualistiese gemeenskap. Aangesien ekologiese en evolusionêre meganismes onafhanklik is van mekaar, het ons die raamwerk van *aanpasbare dinamika* gebruik. Ons het gevind dat die goedgeorganiseerde strukturele patrone wat in die mutualistiese netwerke waargeneem word, soos byvoorbeeld ŉ hoë genestheid en sterk kompartementalisering, kan na vore kom wanneer interaksies eienskap-afhanklik is en die bekombaarheid tot intra en kruis trofiese hulpbronne gekontroleer word. Verder het ons ook gevind dat mutualisme ŉ belangrike rol speel in die volhoubaarheid van evolusionêre stabiliteit en die produktiwiteit van ‘n gemeenskap. Maar, die evolusionêre trajek van funksionele eienskappe in ŉ mutualistiese gemeenskap kan bi-stabiliteit en bi-furkasie ondervind as die mutualistiese interaksies te gespesialiseerd is. In so ŉ geval kan mutualisme ŉ geleentheid skep vir indringerspesies in ŉ leë nis. Biologiese indringing wat ŉ sekere gedeelte van die leë nis teiken kan tot sterk direksionele seleksie in die gemeenskap lei. Verder, ŉ indringerspesie wat ander eienskappe het as die inheem sespesies en ŉ vlak van interaksie spesialisasie ewe aan die inheem sespesie is meer geneig om die gemeenskap te betree. Die struktuur van die ontvanger gemeenskap, soos die nes en kompartement, is nie ŉ primêre determinant van indringerheid nie as daar na ander mates gekyk word, soos byvoorbeeld robuustheid, veerkragtigheid en versteurbaarheid. Gevolglik

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argumenteer ons dat die interaksie tussen ekologiese en evolusionêre meganismes deur middel van eienskapbemiddeling, lig kan werp op belangrike vrae in mutalistiese netwerke.

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Dedications

To my Neny

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List of publications

The following publications were developed during the course of this doctoral dissertation (2012- 2015):

Minoarivelo, H.O., Hui, C., Terblance, J.C., Kosakovsky, P. & Scheffler, K. (2014). Detecting phylogenetic signal in mutualistic interaction networks using a Markov process model. Oikos 123: 1250–1260.

Hui, C., **Minoarivelo, H.O.**, Nuwagaba, S. & Ramanantoanina, A. (2015). Adaptive diversification in coevolutionary systems. In: Pontarotti P (ed) Evolutionary biology: biodiversification from genotype to phenotype.Springer, Berlin, pp 167–186.

Minoarivelo, H.O. & Hui, C. (2015). Trait-mediated interaction leads to structural emergence in mutualistic networks. Evol. Ecol., doi:10.1007/s10682-015-9798-z.

Minoarivelo, H.O., Diedericks, G. & Hui, C. (2015). An introduction to phylogenetic analysis and modelling in ecology. Computational Ecology and Software 5: 328-339.

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Hui, C., Richardson, D.M., Landi, P., **Minoarivelo, H.O.**, Garnas, J. & Roy, H. (2015). Defining invasiveness and invasibility in ecological networks. Biological Invasions, submitted

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CHAPTER 1

Introduction

"Mathematics without natural history is sterile, but natural history without mathematics is muddled"

John Maynard Smith

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1- Background

Mutualism

Flying among orchid plants is a long-proboscis moth, trying to access the nectar of the orchid flowers. Such a scenario is a well-known example of mutualism studied by Darwin back in 1862 (Darwin 1862). In this pollination syndrome, the moth, later known to be the sphinx moth *Angraecum sesquipedale*, pollinates flowers of the Madagascan orchid *Xanthopan morganii praedictaand* and in return is rewarded with the sugar-rich nectar from the orchid. Mutualism, a sort of positive interaction from which pairs of interacting species gain reciprocal benefit, is widely spread in nature. All species on earth are believed to be involved in at least one mutualistic interaction (Bronstein et al. 2004). Being a provider of ecosystem services, mutualistic interactions are also known to enhance the stability of the entire ecosystem (Bronstein 2001). For instance, interactions between flowering plants and their animal pollinators or between fruit trees and their animal dispersers are crucial for the maintenance of ecosystem functioning. In a specific community, several species often engage in multiple interactions, forming a complex ecological network. Interactions in mutualistic networks are known to be well organized in specific patterns (Bascompte & Jordano 2007). Such a level of organization requires that complex ecological and evolutionary processes underlie the assembly of mutualistic networks. Although mutualism has long been studied, ecological and evolutionary processes governing mutualistic communities are still to be elucidated.

The ecology of mutualism

The ability of a species to gain from interacting with others affects its fitness and subsequently the rate at which its population grows. Mutualistic interactions contribute positively to individual fitness of the interacting pairs by provision of benefits. However, gain from mutualism highly depends on how frequent the interaction is. The frequency of an interaction itself is determined by how specialized the interaction is, i.e. by the relative dependence of the interacting pair upon each other. Indeed, mutualistic interactions are often classified according to the specialization of the interaction. In obligate mutualisms, interacting partners fully depend on each other and each partner cannot survive without the presence of the other. In facultative mutualisms, partners gain fitness benefit from the mutualism but can survive and reproduce on their own. The well-organized pattern observed

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in mutualistic networks (Bascompte & Jordano 2007) is mainly about how interaction specialization is distributed among species.

In community ecology of mutualism, a well-established core of research mainly focuses on exploring the asymmetric structure of mutualistic networks. While some studies investigate on the explanation behind such asymmetric structures (e.g. Vazquèz et al. 2007; Olesen et al. 2007; McQuaid & Britton 2013; Minoarivelo et al. 2014), others concentrate on a more conservation-oriented point of view by exploring the implication of such structures on the persistence and maintenance of mutualistic communities (e.g. Okuyama & Holland 2008; Bastolla et al. 2009; Thébault & Fontaine 2010; Rohr et al. 2014). Evolution retains an important role regarding the persistence of mutualistic interactions.

Mutualism and evolution

Mutualism has shaped, and is still shaping life on earth. Ever since Darwin (1862), mutualism has been acknowledged to be an important driver of evolutionary processes such as polymorphism and adaptive diversification (Kiers et al. 2010; Zhang et al. 2013). For instance, the yucca moth *Tegeticula synthetica* is the only pollinator of the Joshua tree *Yucca brevifolia*, whereas the seed of Joshua tree is the only food source for the yucca moth. The speciation in the moth has resulted in the radiation of the flower shape in Joshua trees (William et al. 2008). Darwin has attributed some patterns of mutualistic interactions to coevolution. By changing the interacting functional trait (e.g. the proboscis of pollinators and the floral tube of flowers) through adaptation, the strength of mutualistic interaction between a species pair also evolves and impacts on the overall fitness landscape of the environment. Indeed, when this kind of coevolutionary game of fitness maximization happens among several interacting species within a network, it can lead to rich evolutionary possibilities such as a directional selection or a polymorphism through adaptive diversification (Hui et al. 2015).

A continuing challenge in evolution is to understand how cooperative interactions such as mutualism can still emerge and be maintained despite the evolutionary arms race for fitness maximization. Such a challenge can only be addressed by deepening ecological and evolutionary mechanisms governing mutualistic communities.

Mutualism and stability

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With the exacerbating ecosystem perturbations by natural and anthropogenic means, the structure and functioning of mutualistic interactions are particularly disrupted (Tylianakis et al. 2008, Burkle & Alarcón 2011; Sandel et al 2011). At a rapid ecological time scale, interaction patterns are altered and population densities of mutualistic communities are affected. At a slow evolutionary time scale, selective pressures are altered and adaptation to the changing environment can drive strong evolutionary responses. Intrusion of novel interactions through the process of biological invasion constitutes one of the main threats to ecosystem functioning. Mutualism is known to feedback positively on the stability of a community in the face of such perturbations (Thébault & Fontaine 2010; Rohr et al. 2014). However, species in a community are under different and often conflicting selective pressures imposed by different interactions such as competition and predation. It then becomes interesting to explore the contribution of mutualism to both the ecological and evolutionary stability of a community.

2- Thesis overview

Although operating at a different time scale, ecological and evolutionary processes are intertwined and deserve to be studied simultaneously. In this thesis, we make use of the interdependence of mechanisms governing the ecology and the evolution of mutualistic networks so as to explore patterns of their emergence and their stability. Indeed, we assume that evolutionary changes in functional traits affect the way species interact and subsequently the behaviour of population densities. In return, functional traits change in response to a frequency-dependent selection from changing population densities. The focus of this thesis is mostly theoretical and model-based. The approach uses a set of differential equations to describe the dynamics of population densities and traits in a network of facultative mutualistic interactions. In addition to this introductory chapter, this thesis comprises five additional ones.

Chapter 2 is devoted to investigating the role of mutualism in shaping the stability and trait structure of a mutualistic network. More explicitly, this chapter deals with the contribution of mutualism in generating polymorphism and pattern of trait alignment.

In Chapter 3, we focus on the possible evolutionary trajectories of functional traits in a mutualistic community. We also focus on an unpredictable evolutionary scenario in which empty ecological niches are created, making the community susceptible to invasion.

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Chapter 4 explains how the well-documented asymmetric structure of mutualistic networks can emerge when interaction patterns are determined by functional traits.

The stability of mutualistic networks in the face of biological invasion is discussed in Chapter 5. It deals with identifying characteristics of a successful invader and structures of a recipient mutualistic community that are prone to invasion.

Finally, Chapter 6 serves as a synthesis of the main results and gives suggestions on future research perspectives within the scope of mutualistic interactions.

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CHAPTER 2

Diversification and trait alignment in mutualistic networks

"In considering the origin of species, it is quite conceivable that a naturalist ,reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts, might come to the conclusion that species had not been independently created, but had descended, like varieties, from other species."

Charles Darwin, In *The Origin of Species*

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ABSTRACT

Ecological and evolutionary changes observed in mutualistic networks are shaped by several mechanisms such as intra-trophic competition and co-evolutionary selection. In this study, we explore how those mechanisms affect diversification, system stability and trait alignment. In order to tackle simultaneously the analysis of both ecological and evolutionary processes in a mutualistic network, we followed the adaptive dynamics theory. Using the Lotka-Volterra approach, we built an eco-evolutionary model and simulated ecological dynamics of the population as well as evolutionary dynamics of a phenotypic character through time. Depending on the initial trait values taken by the system, two possible scenarios were observed in our study: whether the system prioritizes benefits given by intra-trophic resource or the system prioritizes benefits given by mutualistic interactions. Diversification and overall biodiversity are mostly enhanced by a strong frequency-dependent competition while mutualism plays a stronger role in evolutionary stability and ecological productivity. Pattern of trait alignment is strongly dependent on the evolutionary scenario adopted by the system. However, mutualism is shown to enhance a better trait alignment than intra-trophic competition. Because different initial scenarios in phenotypic evolution can lead to different interpretations of the same observed pattern, it is then important to explore the way phenotypic traits and population have evolved through time. A deep knowledge of the mechanisms driving traits and population dynamics is needed to draw constructive conclusions on community patterns, such as stability, biodiversity and trait alignment.

Keywords: mutualism, adaptive diversification, trait alignment, frequency-dependent competition, eco-evolutionary dynamics

1- Introduction

Mutualistic interactions, such as the reciprocal dependence of plants on their pollinators or seed dispersers, are crucial for the provision of ecosystem services (Jordano 2000, Bronstein 2001). However, the role of mutualistic interactions to ecosystem stability remains elusive. At the evolutionary time scale, mutualistic interactions can act as a stabilizing selection force and often inhibit the potential of diversification (Yonder & Nuismer 2010). It constrains disruptive selection by favouring common traits but suppressing rare ones specifically in weak mutualistic systems (e.g. seed dispersal networks) (Raimundo et al. 2014), contrasting

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the role of intra-trophic competition that often gives advantages to rare traits. As such, studies on the diversification driven by mutualistic interactions are rare, although evolutionary branching can emerge in mutualistic systems even without intra-trophic competition (Doebeli & Dieckmann 2000, Zhang et al. 2013). At the ecological time scale, in contrast, an ecosystem dominated by mutualistic interactions has been shown to be likely unstable and species poor (Yoshida 2003), although a mixture of antagonistic and mutualistic interactions can enhance the stability of species-rich ecosystems (Mougi & Kondoh 2012). Evidently, evolutionary stability and ecological stability are different concepts; it is thus essential to investigate how mutualistic interactions affect ecosystem stability at both the slow evolutionary and the fast ecological time scales.

Reciprocal selection of a pair of coevolving mutualistic species, known as Darwin's race, can often lead to the evolution towards matching traits (Anderson & Johnson 2008, Pauw et al. 2009, Zhang et al. 2013). For example, the flower morphology of the genus Heliconia matches the bill shape of their common pollinator Purple-throated Carib (*Eulampis jugularis*) in Lesser Antilles (Telemes & Kresss 2003). Such trait matching between a mutualistic species pair has been observed in both small communities composed of specialised species (e.g. Jousselin et al. 2003, Van der Niet & Johnson 2012) and large communities composed of species with different functions (Guimarães et al. 2011, Nuismer et al. 2012). However, trait matching does not necessarily signify coevolution as the trait evolution in a mutualistic system is not only driven by the mutualistic interaction (Nuismer et al. 2010). As such, a clear understanding of how eco-evolutionary processes and feedbacks affect trait matching or alignment in mutualistic networks is needed.

To address the above questions on how mutualism affects system stability and trait alignment in an ecological network, we need to incorporate the eco-evolutionary feedbacks into an integrated model that permits simultaneous analysis of both ecological and evolutionary processes. While most studies focus on how evolutionary processes shape mutualistic assemblages (Rezende et al. 2007, Vázquez et al. 2009, Minoarivelo et al. 2014), others have explored the role of eco-evolutionary dynamics in shaping the phenotypic traits of a mutualistic species pair (Jones et al. 2009, Nuismer et al. 2010, Zhang et al. 2013). Specifically, the theory of *adaptive dynamics* could be used in this pursuit (Metz et al. 1992, Dieckmann et al. 2004, Dercole & Rinaldi 2008). Adaptive dynamics is a powerful tool for modelling the frequency-dependent trait evolution in a community where the dynamics are

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driven by the feedback loop between fast ecological and slow evolutionary processes (Dieckmann & Law 1996, Geritz et al. 1998, Doebeli & Dieckmann 2000).

To explore the role of mutualism in shaping the stability and trait structure in an ecological network, we here build an adaptive dynamics model for the evolutionary dynamics of an emerging mutualistic network, depicting both the evolutionary dynamics of functional traits and the ecological dynamics of population densities. To simplify the mathematical formulation as in many eco-evolutionary models of mutualism (Doebeli & Dieckmann 2000, Ferriere et al. 2002, Zhang et al. 2013, Raimundo et al. 2014), we here only consider one phenotypic trait per morph species. This trait mediates both the intra-trophic competition and the cross-trophic mutualistic interaction, with the interaction strength a function of the trait difference between interacting species (Nuismer et al. 2010). To this end, we specifically explore four issues regarding the role of mutualism to network stability and trait alignment: (i) the condition for diversification (evolutionary branching) via disruptive selection; (ii) the relative contribution of mutualism vs. competition to disruptive selection during the primary and secondary branching events; (iii) the role of mutualism in supporting system biodiversity and productivity; and (iv) drivers of trait alignment in mutualistic networks.

2- Methods

Ecological dynamics

Let there be n functional morphs of animals and *m* functional morphs of plants. Each functional morph, indexed by *i* for animals and *j* for plants, is characterized by its population density A_i (for $i \in 1,...,n$) and P_j (for $j \in 1,...,m$) respectively. For a pollination syndrome, the functional trait of each morph could represent the proboscis length of the pollinator, or the length of pollen tube of the flowering plant. For a seed dispersal syndrome, the functional trait could represent the body mass or the jaw size of the animal disperser, or the fruit/seed size of the plant. We denote the trait of animal morph *i* by x_i and the trait of plant morph *j* by y_j. The population dynamics of the system is depicted by a Lotka-Volterra model with a Holling (1959) type II functional response, as in Zhang et al. (2011):

$$\frac{dA_i}{dt} = A_i\left(r_A - \frac{r_A \sum_k [\gamma(x_i, x_k) A_k]}{K_A(x_i)} + \frac{\sum_j [b_{A_i P_j} w_{A_i P_j} P_j]}{1 + h \sum_j [w_{A_i P_j} P_j]} \right), \qquad (1a)$$

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$$\frac{dP_j}{dt} = P_j\left(r_P - \frac{r_P\sum_k\left[\gamma(y_j,y_k)P_k\right]}{K_P(y_j)} + \frac{\sum_i[b_{P_jA_i}w_{P_jA_i}A_i]}{1+h\sum_i[w_{P_jA_i}A_i]}\right), \qquad (1b)$$

where r is the intrinsic population growth rate, and h the handling time that animals spend for visiting a plant and digesting the nutrients extracted from the plant; both are assumed to be trait-independent to avoid over-parameterization of the model.

The carrying capacity, K_A and K_P, varies between morphs, representing trait-mediated resource accessibility. Following Doebeli & Dieckmann (2000), we used a Gaussian function for the carrying capacity: $K_A(x_i) = k_A N(x_A^{\max}, \sigma_A, x_i)$, where k_A is a scaling constant, and $N(x_A^{\max}, \sigma_A, x_i)$ the Gaussian density function of trait x_i with the maximum carrying capacity at $x_i = x_A^{\max}$ and the standard deviation σ_A.

The intra-trophic competition function γ is set to let morphs with more similar traits suffer stronger competition. We used a Gaussian function for depicting the competition intensity between morphs (Bürger et al. 2006, Doebeli & Dieckmann 2000, Doebeli & Ispolatov 2011, Raimundo et al. 2014): $\gamma(x_1,x_2) = \exp\left[\frac{-(x_1-x_2)^2}{2\sigma_C^2}\right]$, where σ_C controls the width of the competition kernel.

The cross-trophic mutualistic benefit, b_{AP}, reflects the assumption that matching traits bring to each other high profit and is also assumed to follow a Gaussian function of trait difference: $b_{AP}(x_i,y_j) = c\cdot\exp\left[\frac{-(x_i-y_j)^2}{2\sigma_m{}^2}\right]$, where c is a parameter controlling the magnitude of the mutualistic support, and the parameter σ_m controls the tolerance level of successful interactions to the dissimilarity of involved traits (Nuismer et al. 2010).

The interaction preference of two morphs w_{AP} determines the possibility of interaction after the encounter and is assumed to follow adaptive foraging strategies, depending on both the benefit and the abundance of the involved morphs (Doebeli & Dieckmann 2000). Slightly modifying the adaptive foraging strategy in Egas et al. (2005), we have the following function for the interaction preference: $w_{A_iP_j} = \frac{\left(\sum_k A_k\right)\left(b_{A_iP_j}\right)^\beta}{\sum_k[A_k(b_{A_kP_j})^\beta]}$,

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where β is a parameter that determines whether the interaction is optimal (>>1), suboptimal (=1) or neutral (=0). The summation term $\Sigma_k A_k$ in the numerator is for normalization. All terms in Eq.(1b) can be mirrored from above formulation.

Adaptive dynamics

Functional traits of interacting morphs are subject to mutations. Mutation normally happens at a low rate so that the populations can be considered at their ecological equilibriums when the mutation occurs (Doebeli & Dieckmann 2000). We only considered the non-trivial strictly positive and asymptotically stable equilibrium points of the system ($\tilde{A}_i(x_i, y_j)$ and $\tilde{P}_j(x_i, y_j)$). When a mutation enters the system, the resident morphs and the mutant undergo an intra-trophic competition determined by Eq.(1). Let x_i' and y_j' be the mutant trait of animal morph *i* and plant morph *j*, and let $X = (x_1,...,x_n)$ and $Y = (y_1,...,y_m)$ the trait vectors of the resident morphs. We can define the invasion fitness of the rare mutants as their per-capita growth rates when setting their initial densities to be negligible:

$$f_A(X,Y,x_i') = r_A - \frac{r_A \sum_k \left[\gamma(x_i', x_k)\tilde{A}_k\right]}{K_A(x_i')} + \frac{\sum_j b_{A_i'P_j} w_{A_i'P_j} \tilde{P}_j}{1 + h\sum_j w_{A_i'P_j} \tilde{P}_j}, \qquad (2a)$$

$$f_P(X,Y,y_j') = r_P - \frac{r_P \sum_k \left[\gamma(y_j', y_k)\tilde{P}_k\right]}{K_P(y_j')} + \frac{\sum_i b_{P_j'A_i} w_{P_j'A_i} \tilde{A}_i}{1 + h\sum_i w_{P_j'A_i} \tilde{A}_i}. \qquad (2b)$$

The selection gradient, defined as $g_{A_i}(X,Y) = \partial f_A(X,Y,x_i')/\partial x_i'|_{x_i'=x_i}$ and $g_{P_j}(X,Y) = \partial f_P(X,Y,y_j')/\partial y_j'|_{y_j'=y_j}$, determine the direction of trait evolution, and an evolutionary singularity is defined as the traits $(\tilde{x}_i, \tilde{y}_j)$ when the selection gradient disappears. The evolutionary dynamics of the functional traits can be depicted by the canonical equations of adaptive dynamics (Dieckmann & Law 1996):

$$\frac{d}{dt}\begin{pmatrix} x_i \\ y_j \end{pmatrix} = \begin{bmatrix} m_A \tilde{A}_i g_{A_i}(X,Y) \\ m_P \tilde{P}_j g_{P_j}(X,Y) \end{bmatrix}, \qquad (3)$$

where m_A and m_P are parameters proportional to the rate and variation of the mutation.

An evolutionary branching is to occur in the system provided three conditions are satisfied. First, the singularity $(\tilde{x}_i, \tilde{y}_j)$ should be an evolutionary attractor of directional selection; that is, it is convergence stable. This happens when all eigenvalues of the Jacobian

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matrix of Eq.(3) have negative real parts (see Doebeli & Dieckmann 2000). In our specific system, this means $\partial g_{A_i} / \partial x_i |_{x_i=\tilde{x}_i} < 0$ and $\partial g_{P_j} / \partial y_j |_{y_j=\tilde{y}_j} < 0$. Second, the singularity should represent a fitness minimum to induce disruptive selection and to allow the mutant to invade (Geritz et al. 1998); that is, $\partial^2 f_A / \partial x_i'^2 |_{x_i'=\tilde{x}_i} > 0$ and $\partial^2 f_P / \partial y_j'^2 |_{y_j'=\tilde{y}_j} > 0$. Finally, the mutant and the resident morphs need to coexist to ensure the protection of dimorphism from the evolutionary branching (Geritz et al. 1998); that is, the two morphs can invade each other: $(\partial^2 f_A / \partial x_i^2 + \partial^2 f_A / \partial x_i'^2) |_{x_i'=x_i=\tilde{x}} > 0$ and $(\partial^2 f_P / \partial y_j^2 + \partial^2 f_P / \partial y_j'^2) |_{y_j'=y_j=\tilde{y}_j} > 0$.

Numerical simulation

We numerically solved the population dynamics (Eq.(1)) and the canonical equations of adaptive dynamics (Eq.(3)), with an initial population density of 1, or specified otherwise, for both the plant and the animal, and with different values of initial trait values. To separate the ecological dynamics from the evolutionary dynamics, we multiplied Eq.(3) by a small constant ($=10^{-3}$), as in Landi et al. (2013). Once the system reaches its singularity, the three conditions for evolutionary branching will be examined. If satisfied, a new morph will be added to the system with its trait value slightly different from the resident trait (+0.01) and having a low initial density (10% of its resident population density). The density of the resident morph will be simultaneously updated to be 90% of its original. The process was repeated until the system reached its evolutionarily stable strategy (ESS). For cases where the system has an ESS but took too much computational time to reach some of its singularity, we stopped the simulation at 10^7 evolutionary time steps. Note that there were cases where the system did not have an ESS and the evolutionary branching happened indefinitely; for those cases we stopped the simulation after the system has reached its singularity eight consecutive times, i.e. when the system has been updated eight times.

We focused on the effects of three key parameters on the evolutionary dynamics, including the width of the intra-trophic competition kernel (σ_C), the tolerance to trait difference in a mutualistic interaction (σ_m) and the width of resources accessibility (σ_A for animals and σ_P for plants; we keep $\sigma_A = \sigma_P$ for simplicity). Other parameters were fixed in the following analyses for simplicity ($r_A = r_P = 1$; $h = 0.1$; $\beta = 1$; $c = 0.1$; $x_A^{\max} = 3$; $k_A = 400$; $y_P^{\max} = 2$; $k_P = 300$; $m_A = m_P = 10^{-3}$); preliminary tests showed that the results were robust for different values of these parameters. We simulated the evolutionary dynamics for two sets of initial values of morph

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density and trait, and for all combinations of σ_A, σ_C and σ_m, ranging from e^{-3} to e, with a multiplicative step of $e^{1/4}$; a total of 9826 runs.

We investigated on the role of mutualistic interactions in generating diversification by comparing the possibility of a first branching event generated by:

(1) The full model (Eq. (1)).

(2) A resource-competition model, i.e. when population dynamics are governed by intra-trophic interactions only; species are assumed to not share cross-trophic mutualistic interactions:

$$\frac{dA_i}{dt} = A_i\left(r_A - \frac{r_A\sum_k[\gamma(x_i,x_k)A_k]}{K_A(x_i)}\right) \quad ; \quad \frac{dP_j}{dt} = P_j\left(r_P - \frac{r_P\sum_k[\gamma(y_j,y_k)P_k]}{K_P(y_j)}\right) \qquad (4)$$

(3) A model in which the resource-competition term is trait-independent; i.e. only benefits given by mutualistic interactions depend on trait values:

$$\frac{dA_i}{dt} = A_i\left(r_A - \frac{r_A\sum_k A_k}{K_A} + \frac{\sum_j[b_{A_iP_j}(x_i,y_j)w_{A_iP_j}(x_i,y_j)P_j]}{1+h\sum_j[w_{A_iP_j}(x_i,y_j)P_j]}\right), \qquad (5a)$$

$$\frac{dP_j}{dt} = P_j\left(r_P - \frac{r_P\sum_k P_k}{K_P} + \frac{\sum_i[b_{P_jA_i}(x_i,y_j)w_{P_jA_i}(x_i,y_j)A_i]}{1+h\sum_i[w_{P_jA_i}(x_i,y_j)A_i]}\right), \qquad (5b)$$

We measured the strength of disruptive selection at a branching point using the curvature of the invasion fitness (Brännstrom et al. 2011). The separate contribution of competition and mutualism to an evolutionary branching was measured as their fraction of the total strength of the disruptive selection, respectively:

$$\left.\frac{\partial^2}{\partial x_i'^2}\left(r_A - \frac{r_A\sum_k[\gamma(x_i',x_k)\tilde{A}_k]}{K_A(x_i')}\right)\middle/\frac{\partial^2 f_A(x_i,y_j,x_i')}{\partial x_i'^2}\right|_{x_i'=\tilde{x}_i},$$

$$\left.\frac{\partial^2}{\partial x_i'^2}\left(\frac{\sum_j[b_{A_i'P_j}w_{A_i'P_j}\tilde{P}_j]}{1+h\sum_j w_{A_i'P_j}\tilde{P}_j}\right)\middle/\frac{\partial^2 f_A(x_i,y_j,x_i')}{\partial x_i'^2}\right|_{x_i'=\tilde{x}_i}$$

The diversity of animals and plants was estimated as the number of emerged morphs when the system reached its ESS or when the simulation was stopped, and the productivity of animals and plants was measured separately as the total densities of all emerged morphs.

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To calculate the level of trait alignment at the end of the evolutionary dynamics, we first identified for each animal morph i the most matching plant morph and assigned D_i their trait difference; similarly, we calculated D_j for each plant morph j. The average distance $D = (\Sigma_i D_i/n + \Sigma_j D_j/m)/2$ was used to indicate the overall trait alignment of the plant and animal morphs. To compare the effect of the three key parameters (σ_A, σ_C and σ_m) on trait alignment, we used the normalized value of D calculated for different combinations of these parameters, $D_N = (\max(D) - D)/(\max(D) - \min(D))$.

3- Results

Alternative evolutionary scenarios

The initial system, consisting of only one plant morph and one animal morph, has at most two convergence stable strategies which can subsequently lead to two different evolutionary scenarios with different first and secondary branching events. When the system only has one convergence stable strategy, the strategy lies between the trait values of optimal resource accessibility for animals and plants (i.e. if $x_A^{\max} > y_P^{\max}$, then $x_A^{\max} > \tilde{x}_i > \tilde{y}_j > y_P^{\max}$) (Fig.1a-c). Evidently, the convergence stable strategy is a compromise between optimal resource accessibility and optimal benefit gain from mutualism.

When there are two convergence stable strategies in the system, the eventual evolutionary scenario depends on the initial condition of the system (i.e. the initial values of morph density and trait). Such alternative evolutionary scenarios exist especially for low tolerance to trait difference (σ_m) and wide resource accessibility (σ_A), but insensitive to the width of competition kernel (σ_C). In one scenario, the morph first evolves towards prioritizing resource accessibility (i.e. close to either $x_A^{\max}$ or $y_P^{\max}$) (*evolutionary scenario I* hereafter; represented by the convergence to closed circles in Fig.1d-f). In the other scenario, the morphs first evolve towards prioritizing mutualistic interaction (i.e. converging to matching traits [the diagonal on the phase portrait]) (*evolutionary scenario II* hereafter; represented by the convergence to open circles in Fig.1d-f). An example of the trait evolution for both scenarios under the same parameters is given in Fig.2.

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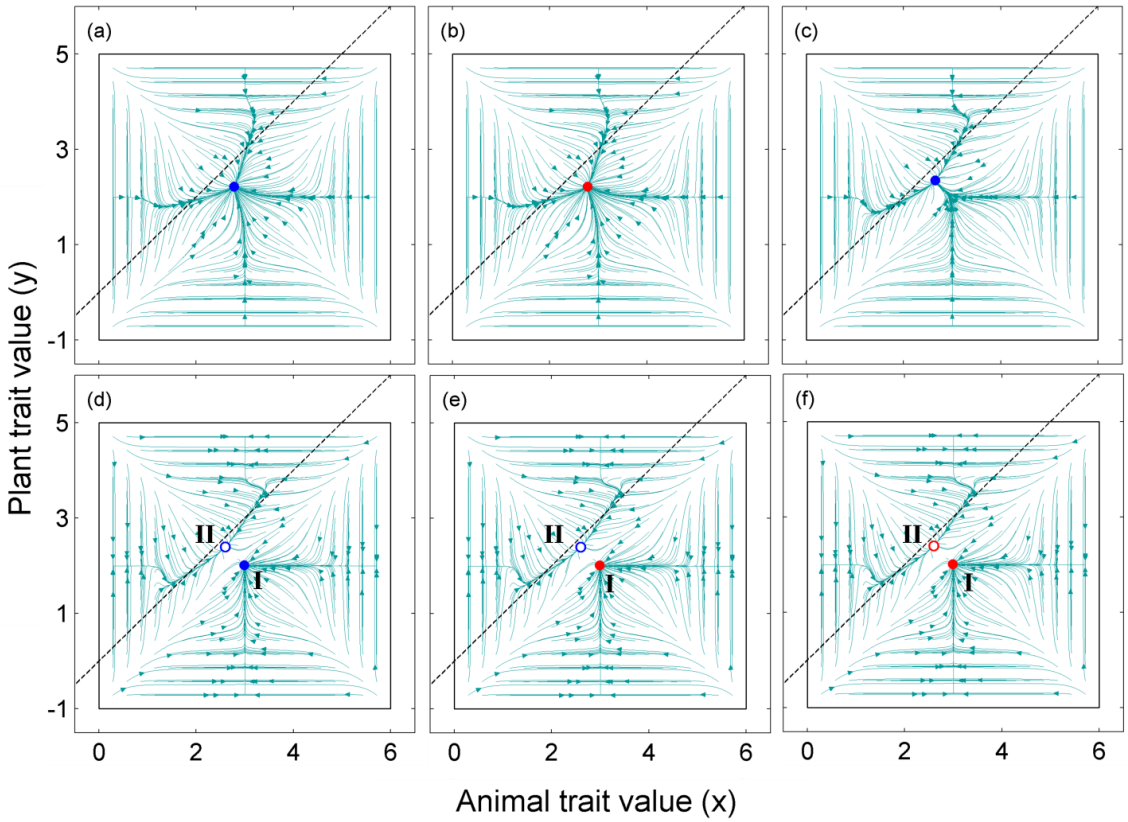

Figure 1: Possible scenarios seen for the convergence-stable strategies that define the first branching event. Blue circles represent ESS while red circles represent disruptive selection. First row shows the existence of only one strategy. Parameters: (a) $\sigma_A = 0.6$; $\sigma_C = 0.6$; $\sigma_m = 0.6$; (b) $\sigma_A = 0.6$; $\sigma_C = 0.47$; $\sigma_m = 0.6$; (c) $\sigma_A = 0.6$; $\sigma_C = 0.47$; $\sigma_m = 0.37$. Second row shows the existence of two strategies. In the second row, closed circles represent *evolutionary scenario I*, open circles represent *evolutionary scenario II*. Parameters: (d) $\sigma_A = 0.6$; $\sigma_C = 0.78$ $\sigma_m = 0.29$; (e) $\sigma_A = 0.6$; $\sigma_C = 0.47$; $\sigma_m = 0.29$; (f) $\sigma_A = 0.6$; $\sigma_C = 0.29$; $\sigma_m = 0.29$. ; The solid square line delimits the viable trait range according to the carrying capacity. The broken line is the diagonal.

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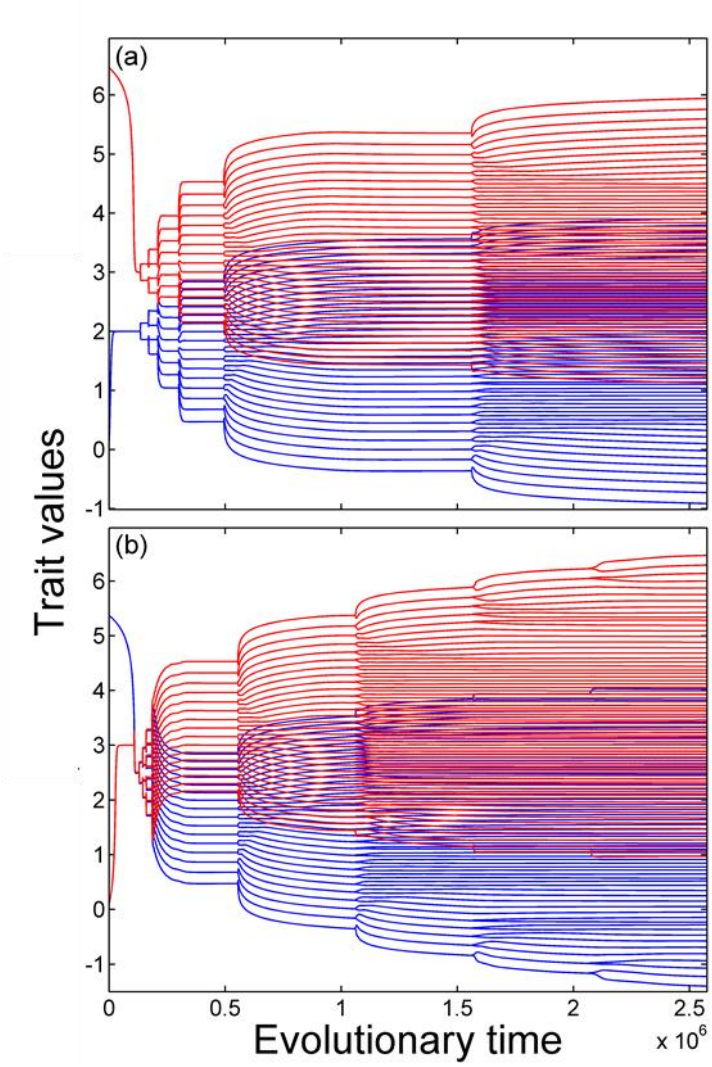

Figure 2: Evolution of phenotypic traits for the animals (red) and the plants (blue) along evolutionary time, for two different initial conditions, using the same set of parameter**:** σ_A = 1; σ_C = 0.08; σ_M = 0.13.

Diversification via disruptive selection

Mutualistic interactions alone cannot produce diversification. On the one side, when the system is modified in such a way that trait-dependence is suppressed in the intra-trophic competition term (Eq.5), analytical study showed that conditions for branching events are never satisfied (Appendix A). On the other side, the parameter zone which shows branching events is larger when cross-trophic mutualistic interactions are switched off (Eq.4) than when the full model is considered (Eq.1) (compare Fig.3 with Fig.4c, f).

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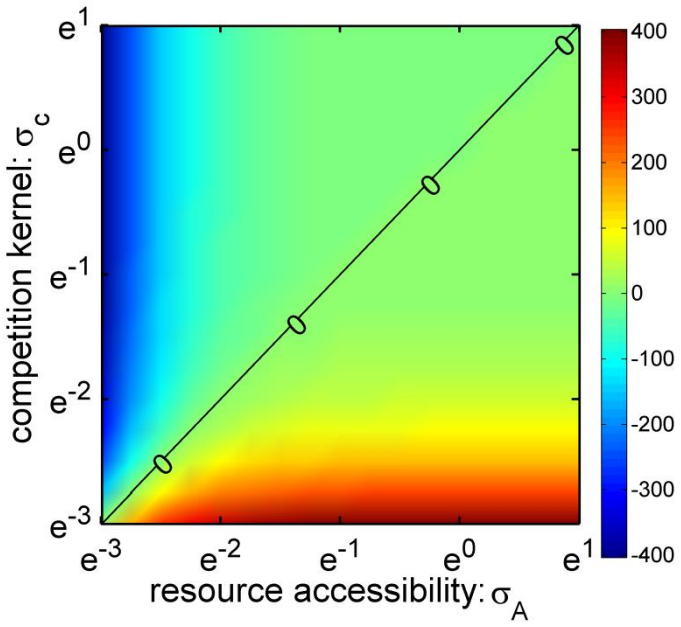

Figure 3: Strength of disruptive selection at a first branching event in the case of a resource-competition model, i.e. when cross-trophic mutualistic interactions are switched off. The black line represents zero strength of disruptive selection.

When considering the full model, evolutionary branching is more likely to happen for wider resource accessibility (σ_A), narrower competition kernel (σ_C), and stronger tolerance to trait difference (σ_M), regardless of the evolutionary scenarios (I or II) (Fig.4). Moreover, we notice that it is more likely to have disruptive selection when the system prioritizes for resource accessibility rather than mutualistic benefits. Indeed, the positive disruptive selection area is larger in Fig.4g than in Fig.4d, and in Fig.4h than in Fig.4e, and in Fig.4i than in Fig.4f. Additionally, diversification is mostly driven by intra-trophic competition (Fig.5), while the contribution of mutualism to diversification is mostly negligible, suggesting that mutualistic interactions act as a neutral force rather than a disruptive force in selection. In some cases, mutualistic interactions can even constrain diversification, with a negative contribution to the disruptive selection. Moreover, mutualistic interactions contribute more to diversification in the evolutionary scenario I than in scenario II as the component of invasion fitness is optimized for harvesting mutualistic benefits which prevents the diversification. The contribution of mutualistic interactions to diversification remains low for subsequent secondary branching events (Fig.S1 in appendix).

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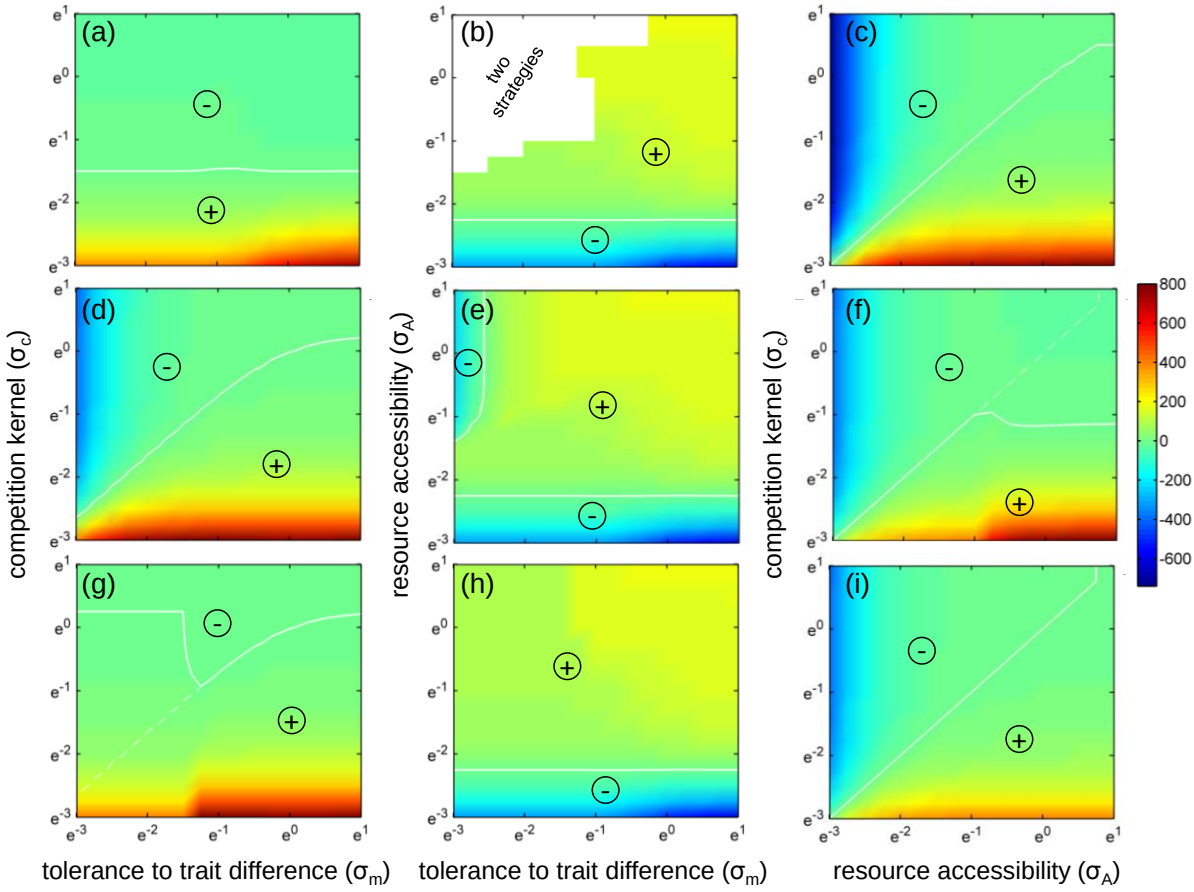

Figure 4: Strength of disruptive selection at the first branching event. The first row shows cases where there is only one evolutionary trajectory irrespective of initial trait values. The second row shows cases where the morphs evolve toward prioritizing mutualistic benefits (evolutionary scenario II) while the third row shows cases where the morphs evolve toward prioritizing resource accessibility (evolutionary scenario I). Zero disruptive selection line is represented by the solid white line. Broken white lines in (f) and (g) show the restricted disruption zone by mutualism. Parameters: (a) $\sigma_A = e^{-1.5}$; (b) $\sigma_C = e^{-2.25}$; (c) $\sigma_m = e^{0.5}$; (d) and (g) $\sigma_A = e^{0.25}$; (e) and (h) $\sigma_C = e^{-2.25}$; (f) and (i) $\sigma_m = e^{-1.5}$.

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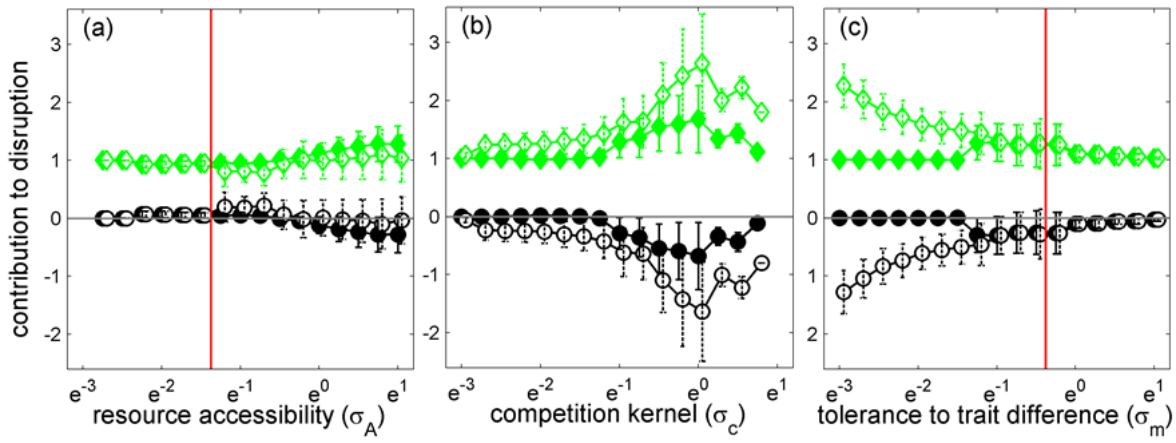

Figure 5: Relative contribution of mutualistic interactions (black circle) and intra-trophic competition (green diamond shape) to the strength of disruptive selection. Values are averaged over all other parameter combinations while one of the parameter is fixed. Bars represent standard deviation. Error bars are a tenth of the standard deviation. *Evolutionary scenario I* is represented by filled circles and filled diamond shapes while *evolutionary scenario II* is represented by open circles and open diamond shapes. Red line separates area of a unique scenario and area of two alternative scenarios. Grey horizontal line represents a zero contribution.

Parameter values that strengthen disruptive selection at the first branching event also resulted in higher numbers of emerged morphs (comparing Fig.4 with Fig.6). Specifically, more morphs emerged with increasing resource accessibility (Fig.6a), while fewer morphs emerged with the increasing width of competition kernel (Fig.6b). Low tolerance level to trait difference can also lead to less emerged morphs, with even fewer morphs emerging from evolutionary scenario II than I (Fig.6c), because low tolerance restricts the occurrence of beneficial mutualistic interactions, leading to more species extinction in scenario II (Fig.S2). When the tolerance level is high, the system only has one convergence stable singularity (i.e. only one evolutionary scenario). Populations are sustained by balancing both the optimal resource accessibility (i.e. traits close to the resource optima $x_A^{\max}$ and $y_P^{\max}$) and the benefit from mutualistic interactions. When the tolerance level is moderate (i.e. high tolerance but not enough to allow all morphs to balance both the resource accessibility and the mutualistic benefit), it is difficult for the scenario-I system, compared to scenario II, to reach its eventual ESS, forming a ditch in the number of emerged morphs (marked by an arrow in Fig.6c).

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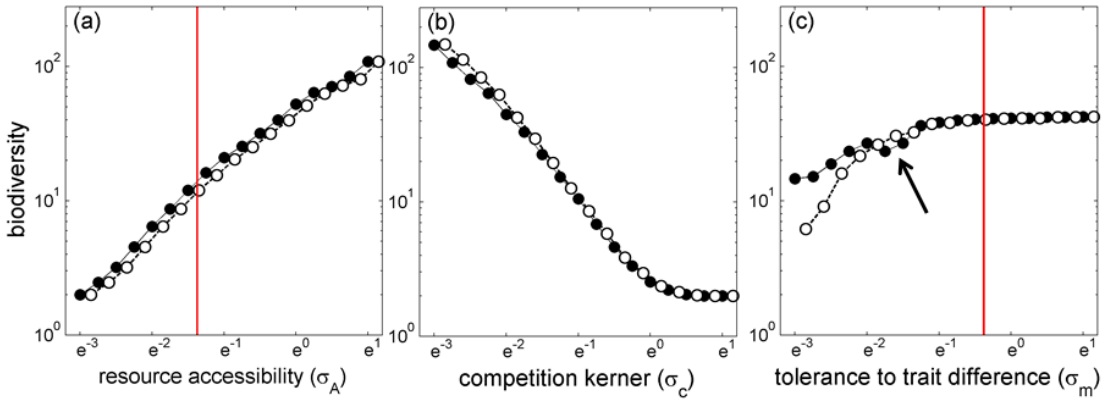

Figure 6: Average (over parameter values) of the resulting biodiversity we obtain from the simulations with respect to one fixed parameter (in a log scale). *Evolutionary scenario I* is represented by closed circles while *evolutionary scenario II* is represented by open circles. The black arrow in (c) indicates a ditch in the number of emerged morphs for *scenario I*.

The number of emerged morphs (biodiversity) is positively correlated with productivity for both the scenario I and II (Fig.7), showing a power-law-like relationship. In the evolutionary scenario I, low tolerance to trait difference (σ_M) further led to the low productivity of the system (Fig.7a and 7b), especially for animals. However, in the evolutionary scenario II, the productivity can be high in the system with low tolerance (Fig.7c and 7d). This suggests that, when the tolerance is low, the benefit from mutualism is insufficient to maintain a high biodiversity, but the system productivity is still enhanced from the mutualistic benefit.

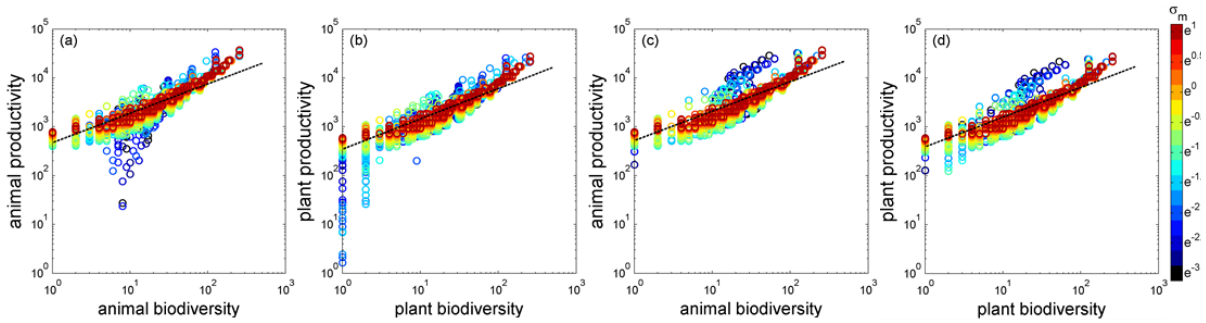

Figure 7: Productivity with respect to biodiversity (log-log scale). Each circle represents one parameter combination. Circles are coloured according to the level of tolerance to traits difference (σ_M). The black dashed line represents the power-law fit to the data. (a) and (b): *evolutionary scenario I*; (c) and (d): *evolutionary scenario II*.

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Trait alignment

Trait alignment between animals and plants is higher when the system sustains itself more heavily on the mutualistic benefit (scenario II) rather than on resource accessibility (scenario I) (i.e. open circles above closed circles in Fig.8). It confirms that mutualistic interactions can reinforce coevolution by inducing greater trait similarity.

In the evolutionary scenario I where the system prioritizes for resource accessibility, the level of trait alignment eventually decreases with the increasing width of resource accessibility (σ_A) (Fig.8a). With wider resource accessibility, traits that are far from the resource optimum can still emerge from the system (Fig.S3a), reducing the overall trait alignment. In contrast, in the evolutionary scenario II, traits become more aligned with the increasing width of resource accessibility (Fig.S8a). As the width of resource accessibility increases, the average trait value of the emerged morphs tends to depart from its respective resource optimum and converge to the average trait value of the interacting partners (Fig.S3b). Consequently, narrow width of resource accessibility may restrict trait alignment because only morphs close to their resource optimum can survive.

Similarly, in the evolutionary scenario I, low tolerance to trait difference reduces the level of trait alignment (Fig.8c). In this case, the traits that are far from both the resource optimum and the average of the interacting partners become common (Fig.S3c), reducing the level of trait alignment. In evolutionary scenario II, when the tolerance to trait difference is low (small σ_m), the average trait value in a morph is more likely to approach the average trait value of the mutualistic partners (Fig.S3d), improving the trait alignment (Fig.8c). In addition, narrower competition kernel (σ_C) can enhance trait alignment (Fig.8b) as a narrower competition kernel induces more morphs which requires more benefits from mutualism and thus stronger alignment to sustain.

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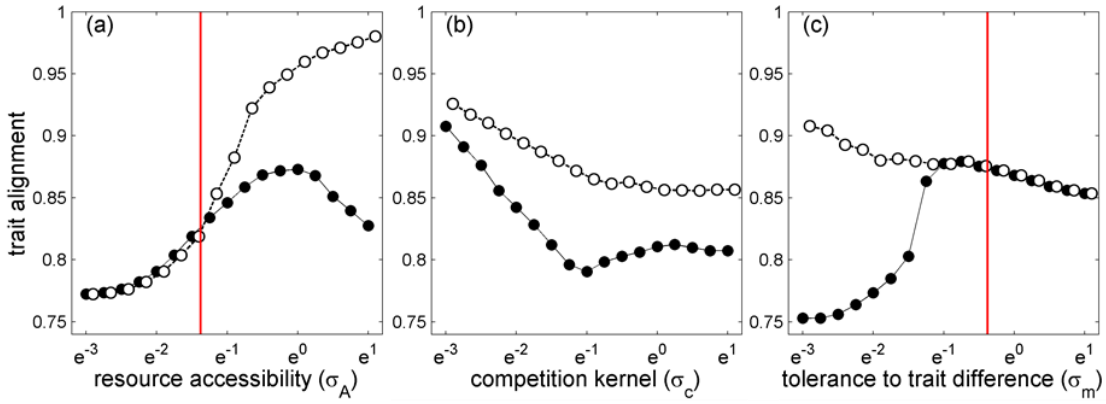

Figure 8: Average (over parameter values) of the degree of alignment between the plant and animal phenotypic traits, with respect to one fixed parameter. *Evolutionary scenario I* is represented by closed circles while *evolutionary scenario II* is represented by open circles.

4- Discussion

Mutualism as a weak disruptive force

Our adaptive-dynamics model comprises both intra-trophic resource competition and cross-trophic mutualistic interactions. The model results in a high number of morphs when the intra-trophic competition is highly trait specific (i.e. strong frequency dependence; small σ_C). To this end, our results are consistent with previous studies on promoting diversification by strengthening frequency dependent intra-specific competition (Dieckmann & Doebeli 1999, Kondrashov & Kondrashov 1999, Bürger et al. 2006, Doebeli & Ispolatov 2011). When the frequency dependence is strongly negative, rare morphs are selectively favoured; a strong frequency dependent selection causes diversification because mutant populations which are initially rare have advantage and increase in frequency forming a new population (Troy & Kyle 2004). In addition, when the frequency dependence is switched off in the competition term, diversification does not happen any longer. This is because the frequency dependent selection driven by mutualistic interactions does not particularly favour either rare or common morphs. The selection favours only morphs that are similar to the morphs of the interacting partners.

When selection is driven predominately by intra-trophic resource competition (i.e. the evolutionary scenario I), diversification normally happens when the resource accessibility is wider than the competition kernel ($\sigma_A > \sigma_C$; Fig.4i) (Dieckmann & Doebeli 1999).

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Interestingly, our model further revealed an alternative path when the selection prioritizes for the benefit from mutualistic interactions (i.e. the evolutionary scenario II). In this scenario, diversification will be promoted when the tolerance to trait difference is higher than the width of the competition kernel ($\sigma_m > \sigma_C$; Fig.4f). When the selection makes a compromise between prioritizing for intra-trophic resource competition and cross-trophic mutualistic interactions (i.e. when the evolutionary scenarios I and II collapse into one), diversification can occur even if the tolerance to trait difference is lower than the width of the competition kernel, $\sigma_m < \sigma_C$; Fig.S4a), but only when the resource accessibility is also wider than the competition kernel ($\sigma_A > \sigma_C$; Fig.S4b), suggesting that resource accessibility and mutualism may reinforce each other in driving diversification.

For most of the parameter combinations, mutualistic interaction in our model is largely an evolutionarily stabilizing force, consistent with previous studies (Nuismer et al. 2010, Raimundo et al. 2014). Nevertheless, some studies of adaptive dynamics did demonstrate the possibility of evolutionary branching in mutualistic systems, either by incorporating obligate mutualism (Ferriere et al. 2007, Jones et al. 2009) or asymmetric interactions (Ferriere et al. 2002, Zhang et al. 2013), creating negative density-dependence in the system. For instance, of the two emerged morphs in Dieckmann & Doebeli (2000), one entirely depends on mutualistic interactions, while the other optimized for resource utilization. The current model differs from the Dieckmann-Doebeli model by incorporating intra-trophic competition and, instead of the proportional effect of a type I functional response, implementing the saturation effect of a type II functional response for mutualistic interactions. In this regard, the behaviour of the Dieckmann-Doebeli model is only a special case where the system only has one unique attractor (Fig.S5). Thus, mutualism is only a weak force for disruptive selection especially when species are also competing for other resources, although it can solely drive diversification (Dieckmann & Doebli 2000, Zhang et al. 2013).

Evolutionary and ecological stability

As of any adaptive-dynamics models (Doebeli & Dieckmann 2000, Ferriere et al. 2002, Landi et al. 2013), we separated ecological dynamics from evolutionary dynamics by setting the former at its equilibrium when the system undergoes an evolutionary change. All ecological equilibriums here are stable as ecological oscillation is impossible in the system. Consequently, ecological stability, defined as the Lyapunov stability (May 1973) and assessed by the leading eigenvalue of the Jacobian of Eq.(1), has already been achieved when

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the system undergoes an evolutionary change. Depending on the stability of the system equilibrium, we have the following three cases of evolutionary stability: (i) ecologically stable, convergence stable [assessed by the leading eigenvalue of the Jacobian of Eq.(3)] and evolutionarily stable [assessed by the curvature of the invasion fitness, Eq.(2)]; (ii) ecologically and convergence stable but evolutionarily unstable; (iii) ecological and convergence stability undetermined, and evolutionarily unstable.

First, the evolutionary equilibrium is both convergence and evolutionarily stable (i.e. a continuously stable strategy), resulting in a low number of emerged morphs. This case is likely to occur with weak frequency dependence in competition, a narrow width of resource accessibility, and a low tolerance to trait difference. The system, in contrast, can be more productive than a high-diversity system, especially in the evolutionary scenario II where the mutualistic benefits are prioritized (Fig.7c and d).

Second, the system does not reach any evolutionary stability but keeps branching indefinitely (i.e. convergence stable but evolutionary unstable). It generates a high number of morphs. Hence, a high biodiversity can be maintained in an ecologically stable system especially when the frequency dependence in competition is strong enough (small σ_C) to ensure diversification while the resource accessibility is wide enough (large σ_A) and the tolerance to trait difference high enough (large σ_m) to sustain a rich biodiversity.

Finally, the system is evolutionary unstable as it has difficulty to reach the convergence stable state, resulting in a low number of morphs. This case is more likely to happen for the evolutionary scenario I, especially when the tolerance to trait difference is moderate. Indeed, when the tolerance to trait difference is low (small σ_m), there exist two evolutionary scenarios. Morphs that are closer to the resource optimum tend to converge close to it for prioritizing for resource competition advantages (evolutionary scenario I). With the increase of the tolerance level to trait difference, morphs (including those close to the resource optimum) are harvesting more benefits from mutualistic interactions. When the tolerance to trait difference is higher than a threshold, there is only one unique evolutionary scenario of a compromise between prioritizing for resource accessibility and mutualistic benefits. However, when the tolerance to trait difference is not low but also not high enough (i.e. intermediate), morphs close to resource optimum are mainly prioritizing for intra-trophic resource accessibility (scenario I) while they are at the same time attracted to prioritize the benefits provided by mutualistic interactions. This situation affects the stability of the system because it becomes difficult to reach convergence stability. Hence, it is essential for its

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stability that the system finds a trade-off between prioritizing either only resource accessibility or the mutualistic benefits, or finding a compromise between compromise between optimal resource accessibility and optimal benefits from mutualism.

Trait alignment

Several drivers affect the trait alignment in the system, and coevolution can be signified by both good and poor degrees of trait alignment, depending on other factors in play. First, observed trait alignment is more likely to be a consequence of coevolution when the system is mainly sustained by mutualistic benefits (i.e. evolutionary scenario II), rather than by intra-trophic resource competition. In some cases of the evolutionary scenario II, mutualistic interactions are the dominant force for trait evolution. Selection directs morphs toward similar traits, enhancing trait alignment via coevolution, especially when the tolerance to trait difference is low (small σ_m). In these cases, high levels of trait alignment for small σ_m (Fig.8c) are strong indicators of the coevolutionary process between animals and plants.

Second, as argued by Nuismer (2010), high degree of trait alignment is not always an evidence of coevolution. It can happen when the plants and animals have similar traits by being subject to selection imposed by the same environment (e.g. convergence evolution from ambient thermal gradient). Since we have set up different values for the parameters controlling the carrying capacity of the animal and the plant, it is unlikely that the trait alignment detected in our model is a consequence of convergence evolution. Moreover, trait alignment can also emerge from one-side selection and trait adaptation, rather than by the reciprocal selection between interacting partners (e.g. Van der Niet & Johnson 2012, Newman et al. 2013). As our model adopted a benefit function that depends only on the trait difference between the two interacting species, the selection imposed by a species on its partner is reciprocal. Thus, our results do not apply to one-side selection, but reciprocal selection that is evident in many communities (e.g. Pauw et al. 2009, Anderson & Johnson 2008).

However, a strong trait alignment in our results does not always indicate a strong coevolutionary process. For example, a high degree of trait alignment is observed in systems having a high diversity of morphs (narrow width of competition kernel σ_C; Fig.8b). The high diversity of morphs in this case precludes large cross-trophic trait differences between the closest pairs.

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Third, a low degree of trait alignment is indicative of mechanisms other than coevolution, in our case mainly by intra-trophic competition. Resource competition often creates dissimilar morphs on the same trophic level (Moen & Wiens 2009); this does not promote mutualistic coevolution (Guimarães et al. 2011; Donatti et al. 2011). For instance, cases, where the system prioritizes for intra-trophic resource accessibility (evolutionary scenario I), show a poor trait alignment from intra-trophic competition (even for small σ_m in Fig.8a and Fig.S3c).

Finally, it can also happen that coevolution does not manifest itself by a strong trait-alignment but rather by trait mismatching (Thompson 2005). For example, in our model when the width of resource accessibility is narrowed (small σ_A), a low degree of trait alignment is observed because species having trait values close to the resource optimum are dominant (Fig.S3a and S3b). However, since the existing species use both intra-trophic resource and mutualistic benefits (in the unique evolutionary scenario), the observed weak trait alignment does not directly imply that the co-evolutionary selection is weak.

In conclusion, our model has shown that diversification in mutualistic networks is a consequence of both intra-trophic competition and mutualistic interactions. While diversification is mostly driven by the former, the latter is largely acting as an evolutionary stabilizer. Initial diversification and subsequent emergence of morphs are more likely to happen with strongly frequency dependent competition (small σ_C), wider resource accessibility (large σ_A) and high tolerance to trait difference (large σ_m). The emerged morphs can show strong trait alignment between plants and animals, depending on whether the system prioritizes for resource accessibility or mutualistic benefits. However, a strong trait-alignment in systems prioritizing for mutualistic benefits is more likely a consequence of coevolution than in systems prioritizing for resource accessibility.

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Appendix A

Branching conditions for a system in which intra-specific competitions are not trait-dependent

The population dynamics in a monomophic population of animals and plants is given by:

$$\frac{dA}{dt} = A\left(r_A - \frac{r_A A}{K_A} + \frac{b_{AP}(x,y) w_{AP}(x,y) P}{1 + h w_{AP}(x,y) P} \right), \qquad \text{(A.1a)}$$

$$\frac{dP}{dt} = P\left(r_P - \frac{r_P P}{K_P} + \frac{b_{PA}(x,y) w_{PA}(x,y) A}{1 + h w_{PA}(x,y) A} \right). \qquad \text{(A.1b)}$$

Descriptions of each term in equation in Eq.(A.1) are given in the main manuscript (Eq.(1)).

The invasion fitness of a rare animal mutant with trait value x' is given by:

$$f_A(x,y,x') = r_A - \frac{r_A A'}{K_A} + \frac{b_{A'P}(x',y) w_{A'P}(x',y) \tilde{P}}{1 + h w_{A'P}(x',y) \tilde{P}} \ .$$

The selection gradient is then given by:

$$g_A(x,y) = \left. \frac{\partial f_A(x,y,x')}{\partial x'} \right|_{x'=x} = \left. \left(\frac{\partial}{\partial x'} \left(\frac{b_{A'P}(x',y) w_{A'P}(x',y) \tilde{P}}{1 + h w_{A'P}(x',y) \tilde{P}} \right) \right) \right|_{x'=x}$$

$$= \left. \left(\frac{\left(w_{A'P} \left(\partial / \partial x' \left(b_{A'P} \right) \right) + b_{A'P} \left(\partial / \partial x' \left(w_{A'P} \right) \right) \right) \tilde{P} \left(1 + h w_{A'P} \tilde{P} \right) - h \left(\partial / \partial x' \left(w_{A'P} \right) \right) \tilde{P}^2 b_{A'P} w_{A'P}}{\left(1 + h w_{A'P} \tilde{P} \right)^2} \right) \right|_{x'=x} .$$

Taking into account that:

$$w_{A'P}\big|_{x=x'} = \left. \frac{(A + A')(b_{A'P})^\beta}{A(b_{AP})^\beta + A'(b_{A'P})^\beta} \right|_{x=x'} = \left. \frac{A(b_{A'P})^\beta}{A(b_{AP})^\beta} \right|_{x=x'} = 1 \ ,$$

and:

$$\left. \frac{\partial w_{A'P}}{\partial x'} \right|_{x=x'} = \left. \left(\frac{\partial}{\partial x'} \left(\frac{(A + A')(b_{A'P})^\beta}{A(b_{AP})^\beta + A'(b_{A'P})^\beta} \right) \right) \right|_{x=x'} = \left. \left(\frac{\partial}{\partial x'} \left(\frac{A(b_{A'P})^\beta}{A(b_{AP})^\beta} \right) \right) \right|_{x=x'} = \left. \left(\frac{1}{(b_{AP})^\beta} \frac{\partial}{\partial x'} \left((b_{A'P})^\beta \right) \right) \right|_{x=x'}$$

$$= \left. \left(\frac{\beta}{(b_{AP})^\beta} \left(\frac{\partial b_{A'P}}{\partial x'} \right) (b_{A'P})^{\beta - 1} \right) \right|_{x=x'} = \frac{\beta}{b_{AP}} \left(\left. \frac{\partial b_{A'P}}{\partial x'} \right|_{x=x'} \right) \ ,$$

then, the selection gradient becomes:

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$$g_A(x,y)=\frac{(1+\beta)\left(\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{x=x'}\right)\tilde{P}\left(1+h\tilde{P}\right)-h\tilde{P}^2\beta\left(\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{x=x'}\right)}{\left(1+h\tilde{P}\right)^2}=\frac{\left((1+\beta)\tilde{P}\left(1+h\tilde{P}\right)-h\tilde{P}^2\beta\right)\left(\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{x=x'}\right)}{\left(1+h\tilde{P}\right)^2}$$

Because the evolutionary dynamics of the animal trait is given by:

$\frac{dx}{dt}=m_A\tilde{A}g_A(x,y)$, the trait value at equilibrium ($\tilde{x}$) is a solution of $g_A(x,y)=0$. Hence, it should be a solution of $\left(\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{x=x'}\right)=0$.

Since $b_{A'P}=c\cdot\exp\left[\frac{-(x'-y)^2}{2\sigma_m^{\,2}}\right]$, then $\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{x=x'}=\frac{-c}{\sigma_m^{\,2}}(x-y)\exp\left[\frac{-(x-y)^2}{2\sigma_m^{\,2}}\right]$.

Consequently, $\left(\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{x=x'}\right)=0 \;\Rightarrow\; \frac{-c}{\sigma_m^{\,2}}(x-y)\exp\left[\frac{-(x-y)^2}{2\sigma_m^{\,2}}\right]=0 \;\Rightarrow\; x-y=0$.

The unique singularity point is such that $\tilde{x}=\tilde{y}$.

To investigate on the possibility of a disruptive selection generated by the system, we check whether the singularity represents a fitness minimum (Geritz et al. 1998).

The second derivative of the invasion fitness is given by:

$$\left.\frac{\partial^2 f_A(x,y,x')}{\partial x'^2}\right|_{x'=x}=\left.\left(\frac{\partial^2}{\partial x'^2}\left(\frac{w_{A'P}b_{A'P}\tilde{P}}{1+hw_{A'P}\tilde{P}}\right)\right)\right|_{x'=x}.$$

If we denote $N=w_{A'P}b_{A'P}\tilde{P}$ and $D=1+hw_{A'P}\tilde{P}$, the second derivative of the invasion fitness at the singularity point is given by:

$$\left.\frac{\partial^2 f_A(x,y,x')}{\partial x'^2}\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}=\left.\frac{\left(\left(\frac{\partial^2 N}{\partial x'^2}\right)D-\left(\frac{\partial^2 D}{\partial x'^2}\right)N\right)D^2-2D\left(\frac{\partial D}{\partial x'}\right)\left(\left(\frac{\partial N}{\partial x'}\right)D-\left(\frac{\partial D}{\partial x'}\right)N\right)}{D^4}\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} \quad \text{, (A.2)}$$

in which:

- $\left.\left(\frac{\partial N}{\partial x'}\right)\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}=\left.\left(\frac{\partial(w_{A'P}b_{A'P}\tilde{P})}{\partial x'}\right)\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}=\left.\tilde{P}\left(w_{A'P}\left(\frac{\partial b_{A'P}}{\partial x'}\right)+b_{A'P}\left(\frac{\partial w_{A'P}}{\partial x'}\right)\right)\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}=\left.\tilde{P}\left(\left(\frac{\partial b_{A'P}}{\partial x'}\right)\left(1+b_{A'P}\frac{\beta}{b_{AP}}\right)\right)\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}$

  $=\tilde{P}(1+\beta)\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}=\tilde{P}(1+\beta)\frac{-c}{\sigma_m^{\,2}}(\tilde{x}-\tilde{y})\exp\left[\frac{-(\tilde{x}-\tilde{y})^2}{2\sigma_m^{\,2}}\right]$.

  Because at the singularity we have $\tilde{x}=\tilde{y}$, then:

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$$\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \frac{-c}{\sigma_m^{\,2}}(\tilde{y}-\tilde{y})\exp\left[\frac{-(\tilde{y}-\tilde{y})^2}{2\sigma_m^{\,2}}\right] = 0\,.$$

Hence, $$\left(\frac{\partial N}{\partial x'}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = 0 \quad . \qquad \text{(A.3)}$$

- $$\left(\frac{\partial D}{\partial x'}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \left(\frac{\partial(1+hw_{A'P}\tilde{P})}{\partial x'}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = h\tilde{P}\left(\frac{\partial w_{A'P}}{\partial x'}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \frac{h\tilde{P}\beta}{b_{AP}}\left(\left.\frac{\partial b_{A'P}}{\partial x'}\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}\right) = 0\,.$$

  (A.4)

- $$\left(\frac{\partial^2 N}{\partial x'^2}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \left(\frac{\partial^2(w_{A'P}b_{A'P}\tilde{P})}{\partial x'^2}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \tilde{P}\left(w_{A'P}\left(\frac{\partial^2 b_{A'P}}{\partial x'^2}\right)+2\left(\frac{\partial b_{A'P}}{\partial x'}\right)\left(\frac{\partial w_{A'P}}{\partial x'}\right)+b_{A'P}\left(\frac{\partial^2 w_{A'P}}{\partial x'^2}\right)\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}$$

  Since

$$\left.\frac{\partial^2 b_{A'P}}{\partial x'^2}\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \left(\frac{\partial}{\partial x'}\left(\frac{-c}{\sigma_m^{\,2}}(x'-y)\exp\left[\frac{-(x'-y)^2}{2\sigma_m^{\,2}}\right]\right)\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \left(\frac{-c}{\sigma_m^{\,2}}\left(1-\frac{(x'-y)^2}{\sigma_m^{\,2}}\right)\exp\left[\frac{-(x'-y)^2}{2\sigma_m^{\,2}}\right]\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}}$$

$$= \frac{-c}{\sigma_m^{\,2}} \quad ,$$

and $$\left.\frac{\partial^2 w_{A'P}}{\partial x'^2}\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \left(\frac{\beta}{b_{AP}}\left(\frac{\partial^2 b_{A'P}}{\partial x'^2}\right)\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \frac{-c\beta}{\sigma_m^{\,2}} \quad ,$$

then, $$\left(\frac{\partial^2 N}{\partial x'^2}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \tilde{P}\left(\frac{-c}{\sigma_m^{\,2}}-\frac{c\beta}{\sigma_m^{\,2}}\right) \quad . \qquad \text{(A.5)}$$

- $$\left(\frac{\partial^2 D}{\partial x'^2}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \left(\frac{\partial^2(1+hw_{A'P}\tilde{P})}{\partial x'^2}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = h\tilde{P}\left(\frac{\partial^2 w_{A'P}}{\partial x'^2}\right)\Bigg|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \frac{-h\tilde{P}c\beta}{\sigma_m^{\,2}} \quad . \qquad \text{(A.6)}$$

By substituting the values given by Eq.(A.3-A.6) into Eq.(A.2), we get:

$$\left.\frac{\partial^2 f_A(x,y,x')}{\partial x'^2}\right|_{\substack{x'=x=\tilde{x}\\ y=\tilde{y}}} = \frac{\left(\tilde{P}\left(\frac{-c}{\sigma_m^{\,2}}-\frac{c\beta}{\sigma_m^{\,2}}\right)\left(1+h\tilde{P}\right)+\frac{h\tilde{P}^2c\beta}{\sigma_m^{\,2}}\right)}{\left(1+h\tilde{P}\right)^2} = \left(\frac{c\tilde{P}}{\sigma_m^{\,2}}\right)\frac{\left(-1-h\tilde{P}-\beta\right)}{\left(1+h\tilde{P}\right)^2}\,.$$

(A.7)

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We can see from Eq.(A.7) that the singularity point $(\tilde{x}, \tilde{y})$ is at fitness minimum if and only if $\left(-1-h\tilde{P}-\beta\right)>0$. Since h, $\tilde{P}$ and β always have positive values, this condition can never be satisfied. It proves that when the competition term is independent of trait values, the system cannot generate disruptive selection.

Supplementary materials

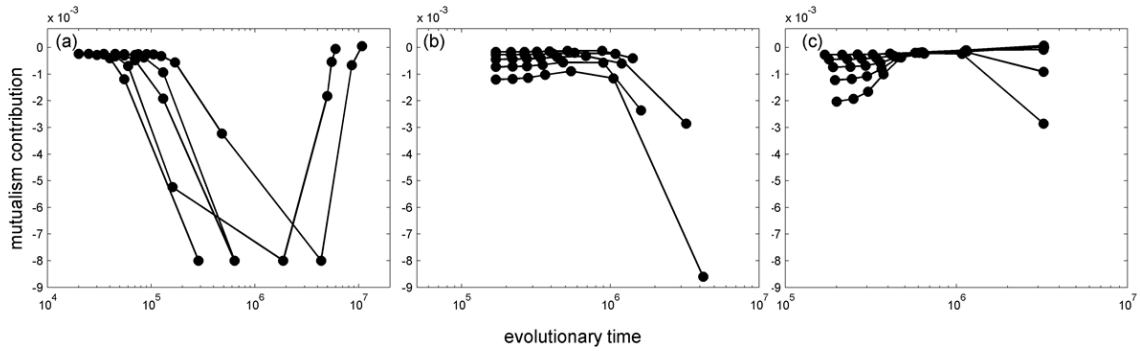

Figure S1: Contribution of the mutualism to diversification events happening along evolutionary time when one parameter is varied. Other parameters: (a) σ_A is varied; σ_c = 0.06; σ_m = 2.7; (b) σ_c is varied; σ_A = 2.7; σ_m = 2.7; (c) σ_m is varied; σ_A = 2.7; σ_c = 0.06.

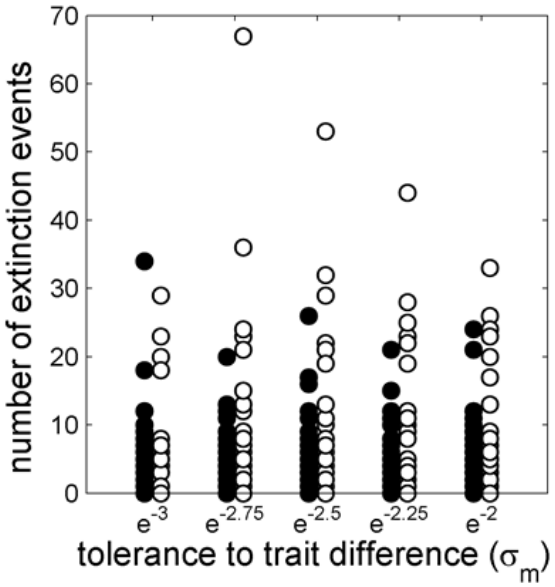

Figure S2: Number of extinction events happening along a simulation with respect to the tolerance to

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trait difference (only range of small σ_m). Each point represents one combination of σ_A and σ_C. Closed circles represent *evolutionary scenario I* while open circles represent *evolutionary scenario II*.

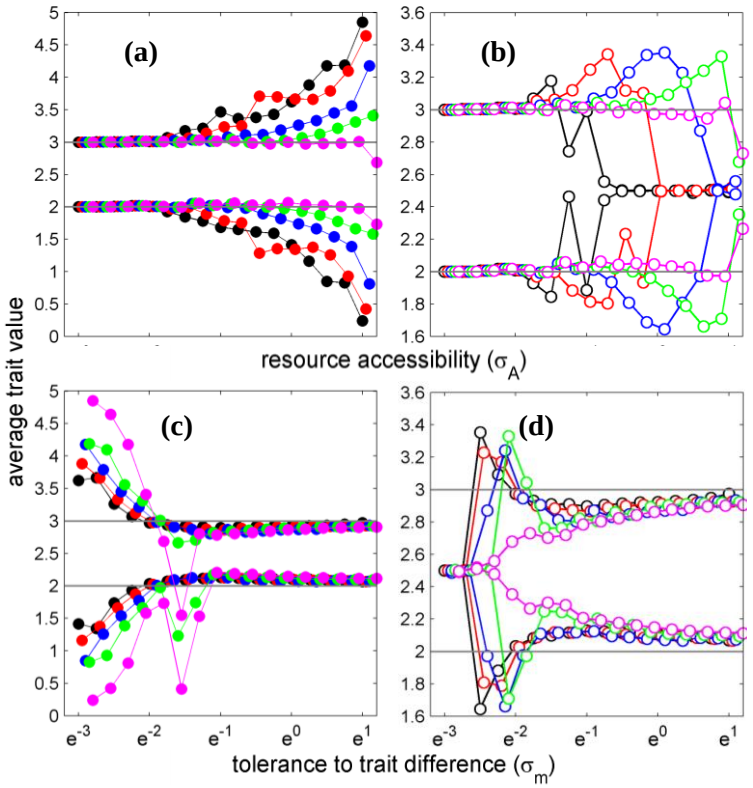

Figure S3: The average trait value of the emerged morphs with respect to σ_A and σ_m. In each panel, average trait values for animals are the ones above (next to the resource optimum x_A^{max} =3), while those for plants are the ones below (next to the resource optimum y_P^{max} =2)

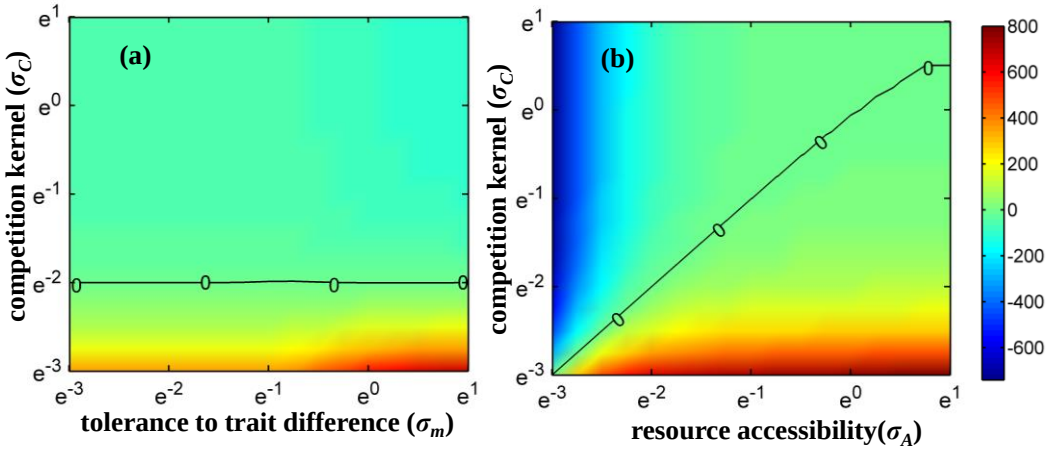

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Figure S4: Strength of disruptive selection at the first branching event, for a case where there is only one evolutionary scenario. Parameters: (a) $\sigma_A = 0.13$; (b) $\sigma_m = 1.65$.

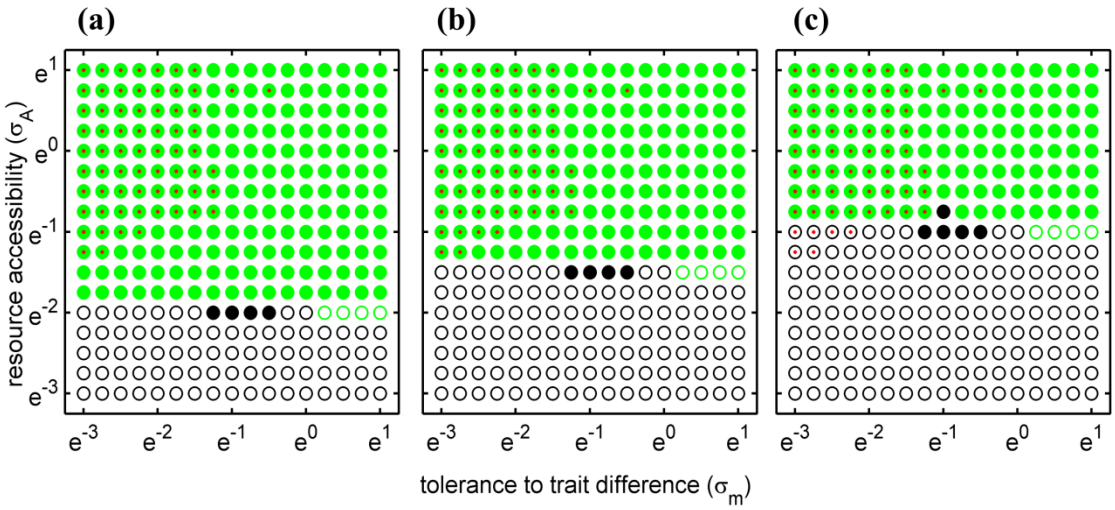

Figure S5: Drivers of disruptive selection for all combinations of the width of resource accessibility (σ_A) and the tolerance to trait difference (σ_m), while the competition kernel is fixed. (a) $\sigma_C = 0.13$; (b) $\sigma_C = 0.22$; (c) $\sigma_C = 0.37$. Green circles indicate that the competition contributes to disruptive selection more than the mutualism. Black circles indicate that the contribution to disruption of the mutualism is higher than that of the competition. Circles are empty when there is no branching event and closed when there is branching event. Circles with a red dot are cases where there are two evolutionary scenarios. We notice that most of the black circles are in the area of a unique evolutionary scenario.

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CHAPTER 3

Specialized mutualistic interaction leads to alternative evolutionary regimes and empty niches for invasion

"At some point in its development, every global civilization will expand until there are no longer new territories available. The civilization will then begin to experience the practical effects of living on a finite planet with finite resources."

Ross Jackson, In *Occupy World Street*

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ABSTRACT

Mutualism is essential for the function and service of ecosystems. With the help from mutualism, species could potentially survive and invade under conditions otherwise unfeasible. Using an adaptive dynamics model, we show that the eco-evolutionary trajectories of a coevolving mutualistic community can experience bistability and bifurcation that are sensitive to the change in the level of tolerance to trait difference in the mutualistic interaction. Low tolerance could lead to extreme scenarios in the system that optimizes for either complete mutualism or resource exploitation. With perturbations, different scenarios under low tolerance converge to a unique community pattern: the bulk of traits exploit resources but only a few with extreme traits rely nearly entirely on mutualism. Mutualism often create opportunity empty niche that peaked at the extreme trait value of the potential partner species. Biological invasions targeting the specific peak of empty niche could lead to interesting results such as strong directional selection in the community and the emergence of new empty niches. We argue that the evolutionary trajectory and the response of specialized mutualistic networks to perturbations and biological invasions can be volatile and should be prioritized in conservation management.

Keywords: bistability, evolutionary trajectories, bifurcation, mutualistic interactions, empty niche, perturbations

1- Introduction

Evolutionary bistability, or the existence of two alternative evolutionary attractors that are dependent on ancestral conditions, has been proposed to be one possible scenario in trait evolution. Although no consensus has been reached on triggers to the existence of evolutionary bistability, it appears more frequent in the trait evolution that is under two, often opposing, selection forces for adaptation. For example, the evolutionary dynamics of pathogenic virulence can exhibit bistability when multiple modes of transmission are available in the system, leading to conflicting selection pressures (van den Bosch et al. 2010; Roche et al. 2011; Boldin & Kisdi 2012). Bistability has also been observed in the population dynamics of species undergoing intra-specific resource competition, where the initial population can converge to a steady state of either low or high abundance if both states confer

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a competitive advantage to locally different populations in the trait space (Dercole et al. 2002).

Besides the aforementioned initial-condition-sensitive bistability, many evolutionary systems have shown the bifurcation of punctuated equilibriums where slight changes in system parameters could lead to a drastic jump of the evolutionary trajectory in the trait space from one to another evolutionary attractor (Dercole et al. 2002; Dercole et al. 2003; Ferrière & Legendre 2013). Parameters responsible for these jumps are often strategic parameters influenced by environmental factors. For example, in a predator-prey coevolutionary model, change in predator efficiency can result into the system bifurcating towards a limit cycle attractor (Dercole et al. 2003). Indeed, the efficiency of a predator in attacking a prey is affected by environmental factors such as humidity or ambient temperature.

Perturbations to the evolutionary trajectory, via large mutation from gene duplication, deletion and translocation or biological invasion of distinct traits, may result in chaotic evolutionary scenarios, especially in the case of bistability and bifurcation. For instance, after a perturbation, the adaptive trait can shift to an evolutionary trajectory leading to its extinction or survival but at a long level of fitness (i.e. an evolutionary trap; Schlaepfer et al. 2002; Zhang et al. 2013). To this end, knowledge of ancestral conditions and eco-evolutionary processes might not be enough to predict the actual evolutionary trajectory in a perturbed system. Resilience of the pre-determined evolutionary trajectory in the face of perturbations also matters (Smallegange & Coulson 2013).

The availability and partitioning of niche, which controls how many and how dense species are packed in a community, can also strongly regulate evolutionary trajectories. Evidently, specialization on different resources can promote species coexistence and thus evolutionary diversification (Dieckmann & Doebeli 1999, Kondrashov & Kondrashov 1999, Bürger et al. 2006, Doebeli & Ispolatov 2011). Not only can niche partitioning affect trait evolution (Laland et al. 1999; Odling-Smee et al. 2013), the reverse also holds: species can affect the environment via niche construction resulting in changes of the fitness landscape (Odling-Smee et al. 2013; Suzuki & Arita 2005; Han & Hui 2014). Mutualism, the reciprocally beneficial interactions between species pair, is known to construct and expand ecological niches through the provision of mutualistic resources and consequently the proliferation of the condition for the survival and coexistence of mutualistic partners (Rodriguex-Cabal et al. 2012; Stachowicz 2012).

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Mutualism is ubiquitous, with most organisms involved in one or more mutualistic interactions during their lifespan (Bronstein et al. 2004); some depend entirely on mutualism for their reproduction and survival (Nilsson 1992; Bronstein et al. 2004). Ever since Darwin (1862), mutualistic interactions have been acknowledged to be an important driver of evolutionary processes, such as leading to polymorphism and diversification (e.g. Kiers et al. 2010; Zhang et al. 2013). The assembly (succession) dynamics of a coevolving mutualistic community is governed by both its evolutionary pathway and the coupling of ecological and evolutionary processes. This means that a mutualistic community can potentially exhibit a strong *priority effect* (May 1977; Young 2001; Fukami 2005) and have alternative evolutionary/succession pathways which are sensitive to initial trait compositions of pioneer species (Dieckmann et al. 1995; Dercole et al. 2003, 2006; Landi et al. 2015).

Through constructing and expanding ecological niches, mutualism can facilitate biological invasions. The establishment of many alien plants has been enhanced by their native mutualistic partners through mechanisms ranging from symbiosis by mycorrhizal fungi, outcrossing reproduction by native pollinators, to facilitated seed dispersal by animal vectors (Richardson et al. 2000; Traveset & Richardson 2014). The fitness and competitiveness of generalist insect invaders can also be facilitated through their interactions with native mutualistic partners (Wilder et al. 2011; Traveset & Richardson 2014). While processes related to biological invasions are mainly operating at the ecological time scale, evolutionary processes can be important in defining the invasibility of ecosystems (Bronstein 2009; Kiers et al. 2010; Saul et al. 2013; Moran & Alexander 2014). Solutions to many debates on invasion depend particularly on the evolutionary relatedness of the native and invasive (Saul et al. 2013), such as Darwin's naturalization hypothesis (Daehler 2001). Disruption to interactions from invasion not only can have ecological impacts, but also alter selective pressure that drives evolutionary response in native species (Bronstein 2004; Traveset & Richardson 2014).

Ecological and evolutionary processes are interdependent. Evolutionary trajectories can be shaped by trait-dependent varying intensity of mutualism (Jones et al. 2009; Nuismer et al. 2010; Zhang et al. 2013), while evolving traits in return mediate ecological interactions (Stang et al. 2009; McQuaid & Britton 2013; Rafferty & Ives 2013). The strength of mutualistic interactions is often mediated by matching functional traits of interacting species (Anderson & Johnson 2008; Pauw et al. 2009; Stang et al. 2009). As such, it is necessary to

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examine the effect of eco-evolutionary coupling on the evolutionary trajectory of a mutualistic community. To this end, the framework of *adaptive dynamics* is a powerful tool for modelling density-dependent trait evolution, where the dynamics of population size and trait are driven by the feedback loop between fast ecological and slow evolutionary processes (Dieckmann & Law 1996; Geritz et al. 1998; Doebeli & Dieckmann 2000).

Here, we adopt a modelling approach to investigate the possible evolutionary pathways of a mutualistic network. Population dynamics and trait evolution are depicted simultaneously in an adaptive dynamics model. To simplify the mathematical formulation (Doebeli & Dieckmann 2000; Ferrière et al. 2002; Zhang et al. 2013), we only consider one functional trait per species. This trait mediates both the intra-trophic competition and the cross-trophic mutualistic interaction, with the interaction strength being a function of the trait difference between interacting partners (Nuismer et al. 2010). Specifically, we examine (i) the alternative evolutionary trajectories of the morphospecies in the mutualistic community; (ii) the stability of the different evolutionary trajectories under trait perturbations; (iii) the eco-evolutionary process by which mutualism can expand opportunity niches for invasion.

2- Method

We assume that the strength of trait-mediated interactions governs the population change rate, and that changing population sizes alters the direction and pressure of frequency- or density-dependent selection which then drives trait evolution. We formulate an adaptive dynamics model that considers the interdependence between population dynamics and trait evolution, and demonstrate the evolutionary and invasion dynamics in a mutualistic community. Specifically, we assume that resource competition becomes intense between two species with similar traits, and that matching traits between a mutualistic pair of animal and plant species confers on them high fitness rewards.

Eco-evolutionary dynamics

Let there be n morphospecies of animals and m morphospecies of plants. Each species is characterized by its population density A_i and P_j, respectively. We denote the trait of animal species i by x_i and the trait of plant species j by y_j. The population dynamics is governed by the intrinsic growth rate (r=1), the intra-trophic competition (γ), and the cross-trophic mutualistic interaction of Holling's type II functional response (Holland et al. 2010; Zhang et al. 2011; Nuwagaba et al. 2015):

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$$\frac{dA_i}{A_i dt} = f_A(x_i) = r_A - \frac{r_A \sum_k \gamma(x_i, x_k) A_k}{K_A(x_i)} + \frac{\sum_j b_{A_i P_j} w_{A_i P_j} P_j}{1 + h \sum_j w_{A_i P_j} P_j}, \quad (1a)$$

$$\frac{dP_j}{P_j dt} = f_P(y_j) = r_P - \frac{r_P \sum_k \gamma(y_j, y_k) P_k}{K_P(y_j)} + \frac{\sum_i b_{P_j A_i} w_{P_j A_i} A_i}{1 + h \sum_i w_{P_j A_i} A_i}, \quad (1b)$$

where h (=0.1) is the handling time. The carrying capacity, K, represents trait-mediated resource accessibility. Following Doebeli & Dieckmann (2000), we used a Gaussian function for the carrying capacity: $K_A(x_i) = k_A N(x_A^{\max}, \sigma_A, x_i)$, where k_A (= 400) is a scaling constant, and $N(\cdot)$ the Gaussian density function of trait x_i with the maximum carrying capacity at $x_A^{\max}$ (=3, unless otherwise stated) and the standard deviation σ_A. For the plant species, k_P = 300 and $y_P^{\max}$ =2 (unless otherwise stated) were taken throughout the study.

The intra-trophic competition function γ is set to let morphs with more similar traits suffer stronger competition (Bürger et al. 2006; Doebeli & Dieckamann 2000; Raimundo et al. 2014): $\gamma(x_1, x_2) = \exp(-(x_1 - x_2)^2 / 2\sigma_C^2)$, where σ_C controls the width of the competition kernel. The cross-trophic mutualistic benefit, b_{AP}, reflects the assortative interaction that matched traits bring high profit, $b_{AP}(x_i, y_j) = c \cdot \exp(-(x_i - y_j)^2 / 2\sigma_m^2)$, where c (= 0.1) is a parameter controlling the magnitude of the maximum mutualistic support, and the parameter σ_m controls the level of tolerance to trait dissimilarity for successful interactions (Nuismer et al. 2010). The interaction preference w_{AP} determines the possibility of interaction after the encounter and depend on both the benefit and abundance of involved morphs (Doebeli & Dieckmann 2000), $w_{A_i P_j} = b_{A_i P_j} \Sigma_k A_k / \Sigma_k A_k b_{A_k P_j}$.

We only consider the non-trivial strictly positive and asymptotically stable equilibrium points of the system ($\tilde{A}_i(x_i, y_j)$ and $\tilde{P}_j(x_i, y_j)$). When a mutation enters the system, the resident morph and the mutant undergo an intra-trophic competition determined by Eq.(1). Let x_i' and y_j' be the mutant trait of animal i and plant j, and let $X = (x_1, ..., x_n)$ and $Y = (y_1, ..., y_m)$ be the trait vectors of the resident morphs. We can define the invasion fitness of the rare mutants at the equilibrium points as their per-capita growth rates when setting their initial densities to be negligible: $f_A(x_i')$ and $f_P(y_j')$, and thus the selection gradient,

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$g_{A_i} = \partial f_A(x_i')/\partial x_i'|_{x_i'=x_i}$ and $g_{P_j} = \partial f_P(y_j')/\partial y_j'|_{y_j'=y_j}$. The evolutionary dynamics of the traits can be depicted by the canonical equations of adaptive dynamics (Dieckmann & Law 1996):

$$\begin{aligned} dx_i/dt &= m_A \tilde{A}_1 g_{A_i} \\ dy_j/dt &= m_P \tilde{P}_1 g_{P_j} \end{aligned}, \qquad (2)$$

where m_A and m_P are parameters proportional to the rate and variation of the mutation (=10^{-3}). An evolutionary branching is to occur provided three conditions are satisfied. First, the singularity $(\tilde{x}_i, \tilde{y}_j)$ should be convergence stable, happening when all eigenvalues of the Jacobian of Eq.(2) have negative real parts (Doebeli & Dieckmann 2000), $\partial g_{A_i}/\partial x_i|_{x_i=\tilde{x}_i} < 0$ and $\partial g_{P_j}/\partial y_j|_{y_j=\tilde{y}_j} < 0$. Second, the singularity should represent a fitness minimum to induce disruptive selection (Geritz et al. 1998), $\partial^2 f_A/\partial x_i'^2|_{x_i'=\tilde{x}_i} > 0$ and $\partial^2 f_P/\partial y_j'^2|_{y_j'=\tilde{y}_j} > 0$. Finally, the mutant and the resident species need to ensure the protection of dimorphism from the evolutionary branching (Geritz et al. 1998), $(\partial^2 f_A/\partial x_i^2 + \partial^2 f_A/\partial x_i'^2)|_{x_i'=x_i=\tilde{x}} > 0$ and $(\partial^2 f_P/\partial y_j^2 + \partial^2 f_P/\partial y_j'^2)|_{y_j'=y_j=\tilde{y}_j} > 0$.

Numerical simulations

We investigated the evolutionary attractors by varying the initial trait values (15 values from 1 to 4 trait units) under different combinations of competition kernel (σ_C), the tolerance to trait difference in mutualistic interaction (σ_m) and the width of resources accessibility (σ_A), ranging from e^{-3} to e with a multiplicative step of $e^{1/4}$. To assess the resilience of observed evolutionary trajectories in the face of perturbations, we added perturbations to the model in two ways. First, traits were perturbed during their evolution by small stochastic noise with a standard deviation of 0.5, brought into the system at a rate of 0.01 per time unit. Second, alien morph was introduced, randomly drawn from the viable trait space at a rate of 0.01 per time unit. The population size of introduced morphs was set to 10% of the minimum resident population density.

We numerically solved the population dynamics (Eq.(1)) and the canonical equations of adaptive dynamics (Eq.(2)). To take into account the time scale separation between ecological and evolutionary dynamics, we multiplied the canonical equations of adaptive dynamics (Eq.(2)) by a small constant (=10^{-3}), as in Landi et al. (2013). As the system of differential equations was stiff, we solved them numerically using the ode15s function in

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MATLAB which implements a variable order method for the integration (Shampine & Reichelt 1997). Once the system reached its singularity, the three conditions for evolutionary branching were examined. If satisfied, a new morph was added to the system with a trait value slightly different from the resident trait (+0.01) and a low initial density (10% of its resident population density). The density of the resident morph was simultaneously updated to be 90% of its original.

3- Results

Alternative evolutionary trajectories

When the system only has one convergence stable strategy, the strategy lies between the trait values of optimal resource accessibility for animals and plants, $x_A^{\max} > \tilde{x}_i > \tilde{y}_j > y_P^{\max}$ (attractor A in Fig.1a). Evidently, the convergence stable strategy is a compromise between optimal resource accessibility and optimal benefit gain from mutualism. When there are two convergence stable strategies in the system (i.e. bistability), the eventual evolutionary trajectory depends on the initial values of population density and trait. Such alternative evolutionary trajectories exist especially for low tolerance to trait difference (σ_m) and wide resource accessibility (σ_A), but insensitive to the width of competition kernel (σ_C). In one scenario (attractor B in Fig.1b), the morphs first evolve towards prioritizing mutualistic interaction, i.e. converging to matching traits $\tilde{x}_i = \tilde{y}_j$ (the diagonal on the phase portrait). In the other scenario (attractor C in Fig.1b), the morph first evolves towards prioritizing resource accessibility, i.e. $\tilde{x}_i$ tends to equal $x_A^{\max}$ and $\tilde{y}_j$ tends to equal $y_P^{\max}$.

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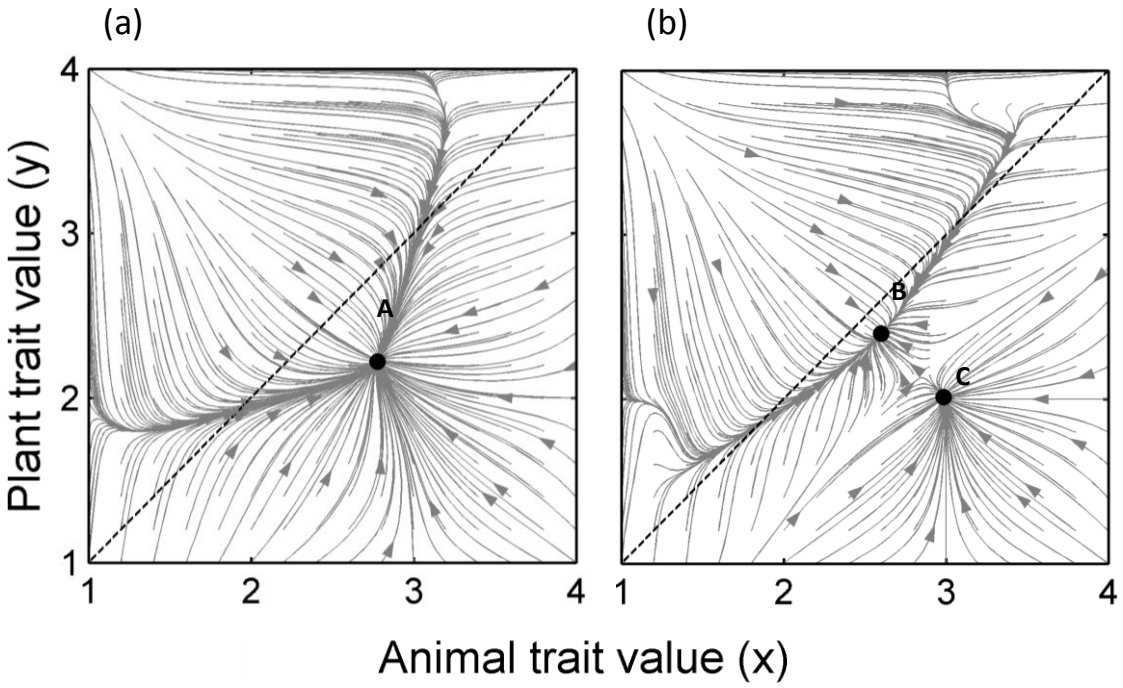

Figure 1: Alternative evolutionary trajectories taken by traits before the first branching event. (a) Only one convergence stable strategy is observed; Parameters: $\sigma_A = e^{-0.5}$; $\sigma_C = e^{-0.75}$; $\sigma_m = e^{-0.5}$. (b) Two convergence stable strategies are observed: the morphs evolve toward either strategy B by prioritizing mutualistic benefits, or strategy C by prioritizing resource accessibility; Parameters: $\sigma_A = e^{-0.5}$; $\sigma_C = e^{-0.75}$; $\sigma_m = e^{-1.25}$. Each of the convergence stable strategies A, B or C can represent either an ESS or a disruptive selection for further evolutionary branching. The broken line represents the diagonal.

Evolutionary trajectories driven by disruptive selection is sensitive to the level of tolerance to trait difference (σ_m). When the tolerance is low, the evolutionary trajectories followed two patterns. First, the subsequent polymorphic system of attractor B in Fig.1b kept prioritizing for mutualistic benefits through strongly aligning animal and plant traits (Fig.2c). Second, the subsequent polymorphic system from attractor A and C in Fig.1 tend to have little trait overlapping (Fig.2a and e), with most evolving separately around their perspective resource optima and only few aligned to gain from mutualistic benefits.

When the tolerance is high, the subsequent polymorphic system of all three attractors behave similarly (Fig.2 second column), utilising both mutualistic benefits and environmental resources. The strong reliance on mutualistic benefits (attractor B) is attenuated with more morphs emerged (Fig.2d), while the optimal use of resource (attractor C) is compensated by

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favouring mutualistic benefits (Fig.2f). With the increase of the tolerance to trait difference (σ_m), the contribution of mutualism to the overall growth rate declined in the subsequent system of attractor B (Fig.S1) but increased in the system from attractor C (Fig.S1). The subsequent system of attractor B undergoes an abrupt shift from optimizing for mutualistic benefit (Fig.2c) to the compromised state (Fig.2d) with increasing tolerance (see Fig.S1 and Fig.S2). By contrast, the subsequent system of attractor C undergoes a rather gradual transition (see Fig.S1 and Fig.S3). With the increase of the tolerance, the system experienced a bifurcation from the bistability scenario into a scenario of single attractor (Fig.S1).

Evolutionary trajectories under perturbation

Under perturbation, all evolutionary trajectories converge to a unique scenario where most plant and animal morphs cluster around their perspective resource optimum (Fig.3), with only a few morphs thriving completely outside their accessible resources and fully relying on mutualistic benefits. The evolutionary trajectories from attractor B are not resilient as evident by the vulnerability to perturbations, with the strong trait matching between animal and plant morphs (Fig.2c) easily lost (Fig.3c and e).

Moreover, under perturbations, the dynamics of trait evolution still differs for low and high tolerance to trait difference. When the tolerance is low, resource exploitation is restricted to the side of maximum accessibility with only a few traits matching each other on the boundaries of trait ranges, leaving apparent empty niches unexploited (Fig.3a, c and e). When the tolerance is high, traits can diversify symmetrically around their resource optimum (Fig.3b, d and f). However, traits that temporally jumped outside the optimum range for resource accessibility from perturbations experienced strong directional selection and were immediately redirected towards resource accessibility. The gap of empty niche between the few traits targeting mutualism and the bulk of traits shrank rapidly with the increase of tolerance (Fig.S4). Perturbations from introducing additional morphs led to similar results (Fig.S5).

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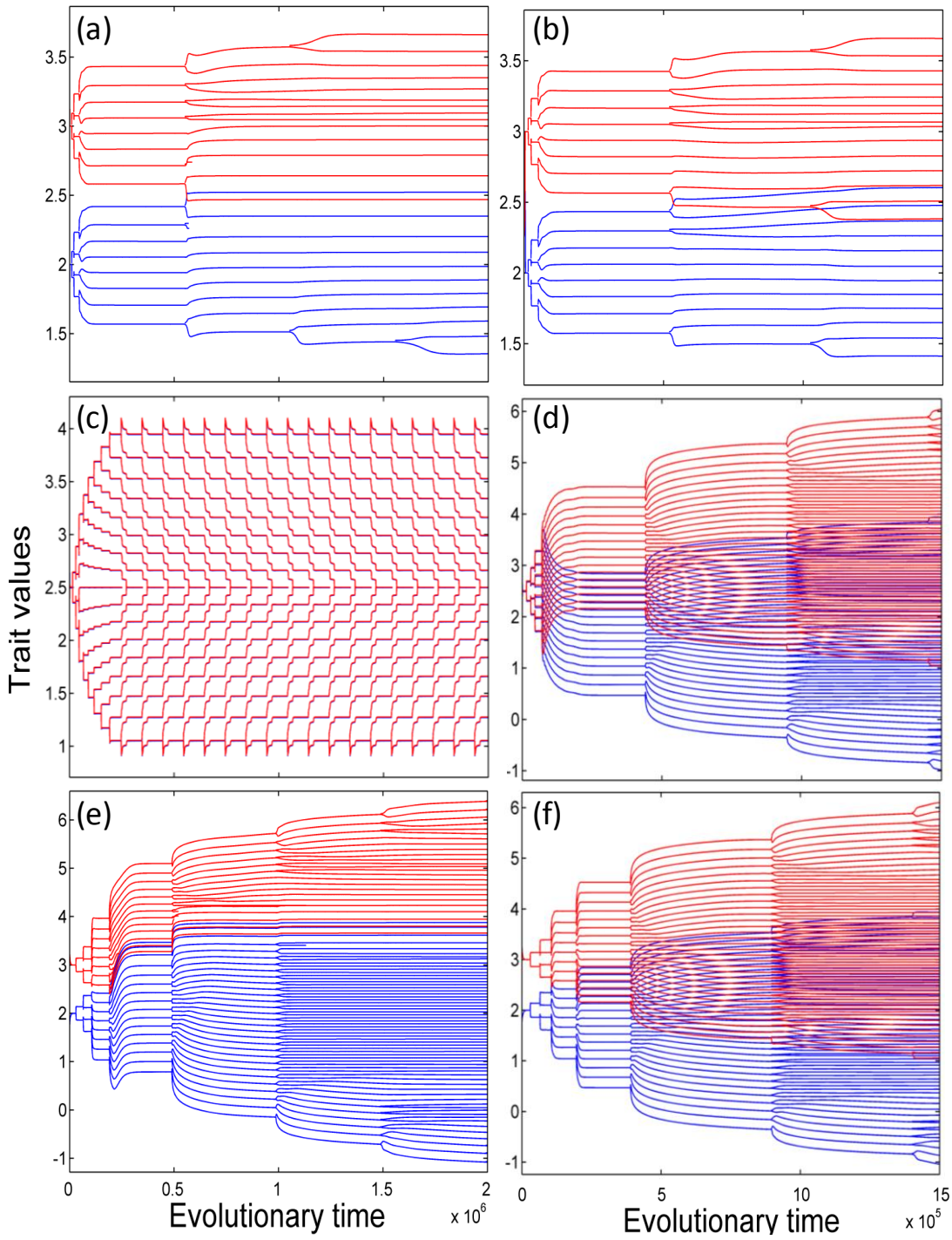

Figure 2: Evolution of phenotypic characters for the animals (red) and the plants (blue). The first row shows cases where there is only one evolutionary trajectory irrespective of initial trait values. Parameters: (a) $\sigma_A = e^{-1.5}$; $\sigma_C = e^{-2.5}$; $\sigma_m = e^{-2.5}$; (b) $\sigma_A = e^{-1.5}$; $\sigma_C = e^{-2.5}$; $\sigma_m = e^{-2}$. The second row shows cases where the morphs evolve toward prioritizing mutualistic benefits while the third row shows cases where the morphs evolve toward prioritizing resource accessibility. Parameters: (c) and (e) $\sigma_A = e^{0}$; $\sigma_C = e^{-2.5}$; $\sigma_m = e^{-2.5}$; (d) and (f) $\sigma_A = e^{0}$; $\sigma_C = e^{-2.5}$; $\sigma_m = e^{-2}$. First column shows cases of a lower

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tolerance to trait difference (σ_m) than for those cases shown in the second column.

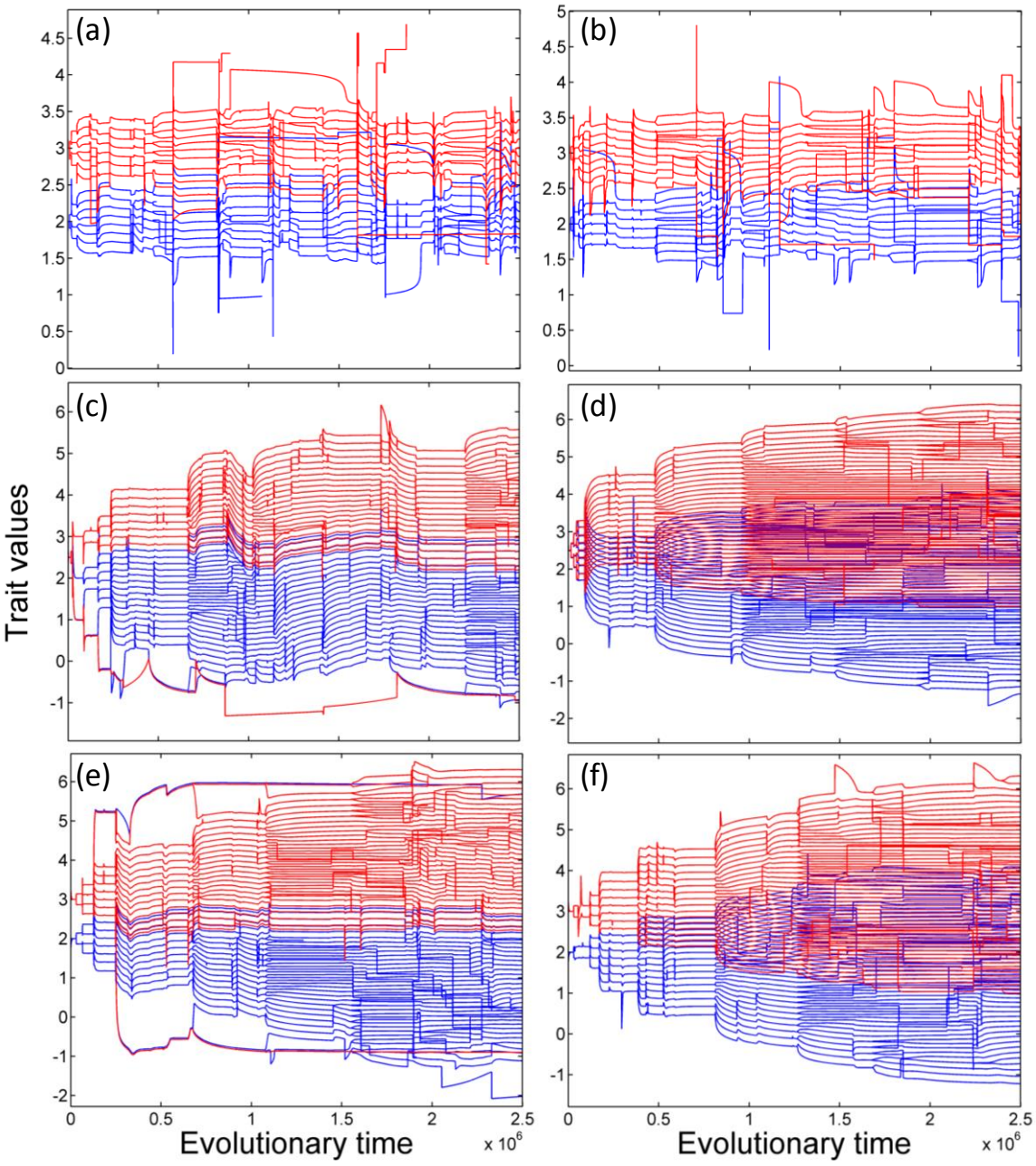

Figure 3: Evolution of trait values for different evolutionary trajectories when the morphs are perturbed by stochastic noises. Animal trait values are in red while plant trait values are in blue. Parameters are as in Fig.2. Perturbations are drawn from a normal distribution with standard deviation of 0.5 and brought into the system at a rate of 0.01.

Empty niches for invasion

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When the interactions between mutualistic partners are highly specialized (low tolerance with small σ_m), overlapped animal and plant traits become highly aligned (Fig.4a). With the support from strong mutualism, these aligned traits can possess much higher population densities than other traits with no mutualistic partners. The strong asymmetric competition from these aligned traits can create a barrier that prevents other morphs to further explore mutualistic benefits through small mutations. Consequently, an empty niche is left unexploited on each side of the animal and plant trait space. Apparently, these empty niches can be invaded due to their positive invasion fitness, with the peak of the empty niche aligned with the uttermost trait of the other species group (pink zone in Fig.4a).

Biological invasions that fill up all fitness peaks of empty niches could cause a drastic change in the evolutionary trajectory (Fig.4b, 4c and 4d). With the introduction of a trait matching perfectly with the peak of empty niche on each side, the system could quickly converge to the scenario of strong trait alignment as seen in Fig.2c, leading to a climax community with no empty niches for invasions (Fig.4b). If the introduced traits do not perfectly align with the peak of empty niches, the system could experience a strong directional selection, with a new peak of empty niches emerged at the extreme trait value of the other species group and thus the community ready for a new round of invasion (Fig.4c). It could also happen after the introduction of traits at the peak of empty niches that the introduced trait forms a strong mutualistic partner with extreme traits, leaving a new empty niche from the pack of traits with no mutualistic partners (Fig.4d). Overall, when the tolerance to trait difference is low, mutualistic interactions become extremely specialized, leaving empty niches for invasion. New and distinct empty niches are likely to be created after the invasion when the system often also undergoes strongly directional selection.

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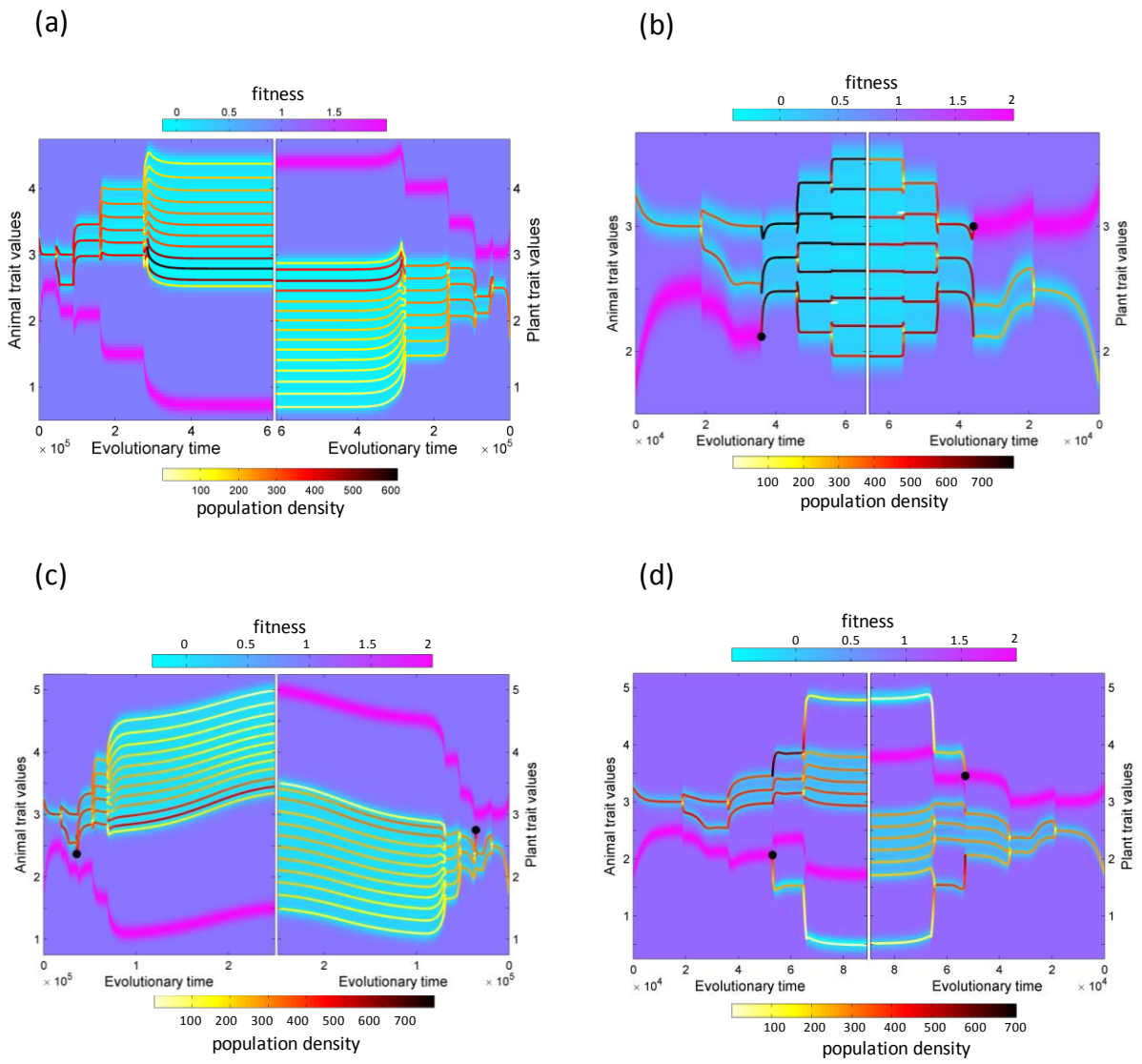

Figure 4: Evolution of trait values of a specialized mutualistic community. (a) Without introduction of alien morph; (b), (c) and (d) with introductions of alien morphs at different locations of the niche space. The fitness landscape is presented as a background colour described in the colour bars at the top. Population densities are described in the colour bars at the bottom. Black dots show where aliens are introduced. Parameters: $\sigma_A = e^{0}$; $\sigma_C = e^{-2.5}$; $\sigma_m = e^{-2.5}$; $x_A^{max} = 3$; $y_P^{max} = 2.5$.

4- Discussion

We have shown that in a mutualistic community where biotic interactions are governed simultaneously by ecological and evolutionary processes, species traits can evolve

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directionally and disruptively towards different trajectories pending on the dominant selection force. Trait evolution can be contingent to the choice of ancestral species on whether to optimize either for intra-trophic resource exploitation or mutualistic benefits. Under perturbations, most traits will only be optimized for resource exploitation but with a few exceptions targeting entirely on mutualism. The level of tolerance to trait difference in the mutualistic interactions constitutes a strong determinant of the evolutionary trajectories. In particular, mutualistic communities that are specialized in their mutualistic interactions (i.e. low tolerance) tend to evolve in such a way that empty niches are left open for biological invasions. Successful invasions often create a strong directional selection and shift the system into an alternative evolutionary trajectory.

The coupling of ecological and evolutionary processes in our system can result in opposing selection forces and thus evolutionary bistability, consistent with previous studies (van den Bosch et al. 2010; Roche et al. 2011; Boldin & Kisdi 2012). As we only considered a single trait that mediates both mutualistic interaction and resource competition, the species was left with often two alternative evolutionary strategies, with one targeting resource optimum and the other trait alignment with mutualistic partners. When the level of tolerance to trait difference in mutualistic interactions is low (i.e. a specialised interaction), the selection force driven by the potential mutualistic benefits is strong, pushing the system to undergo a bifurcation and experience bistability. As such, environmental factors that could affect the level of tolerance, such as rising temperatures, may result in a change in the evolutionary trajectory (Dercole et al. 2003; Ferrière & Legendre 2012).

Under perturbations, we have shown that a perfect trait-matching system is unlikely to be realised. This confirms that traits evolution cannot solely depend on the evolutionary history of ancestral species (Smallegange & Coulson 2013) but is a joint result of biotic interactions and environmental perturbations (in the form of disturbance and stress). Even under perturbations, scenarios where a specialised community creates empty exploitable niches stay robust. This further confirms empirical findings on the role of mutualism on shaping the fitness landscape in such a way that ecological niches are expanded (Rodriguex-Cabal et al. 2012; Stachowicz 2012).

We showed that the creation of empty exploitable niches in mutualistic communities is a result of a sort of barrier created by traits of high density, a manifesto of density-dependent selection at work. The negative density-dependent selection manifested by the

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competitive exclusion (Hardin 1960) suppresses traits adjacent to these high-density traits from exploring available ecological niches. Mutualistic interactions can also pose a positive frequency-dependent selection on traits and give advantage to those that can align with the common traits of their mutualistic partners, leading to a trait convergence in the community (Elias et al. 2008; Guimarães et al. 2011; Nuismer et al. 2012). When the tolerance to trait difference is low, the selection force imposed by each mutualistic partner is particularity strong and narrowly distributed. The presence of both positive and negative frequency-dependent selection resulted in an unpredictable volatile evolutionary trajectory, making the system susceptible to invasion (Richardson et al. 2000; Wilder et al. 2011; Traveset & Richardson 2014).

Furthermore, we showed that exploitation of the empty niches by alien morphs could cause a drastic change in the evolutionary trajectory. The system undergoes a strong directional selection and other empty niches are likely to be created after the invasion. This suggests that the characteristics of mutualistic communities to be prone to invasion could be a result of long eco-evolutionary processes. Moreover, the fate of an introduced morph is dependent not only on its trait value but also on the level of interaction specialization of the community. For example, although alien morphs having trait value not common to the native community could escape from competition, they are able to evolve independently from the rest of the native morphs only provided that they acquire enough support form mutualistic interactions. This case can happen only when the level of tolerance to trait difference in mutualistic interactions is weak (small σ_m; Fig.4d and Fig.S5c, S5e). This means that Darwin's naturalization hypothesis holds only under certain conditions. We also see that introduced morphs having trait values similar to those of native morphs are more advantageous when the selection imposed by mutualism is weak (i.e. for higher level of tolerance to trait difference: large σ_m), contradicting Darwin's naturalization hypothesis. Indeed, these morphs evolve directionally towards the niche space provided by intra-trophic resources instead of running away from competition (Fig.S5d, S5f). Hence, the debate on whether Darwin's naturalization hypothesis holds depends upon the eco-evolutionary experience of the native and introduced species (Saul et al. 2013).

Although we were able to explore ecological and evolutionary explanations behind the creation of ecological niches by mutualism, possible aspects of the response of mutualistic communities to biological invasion were only generally addressed. For instance,

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by assuming that introduced morphs also share the same level of tolerance to trait difference as the native morphs, we assume that a unique level of interaction specialization predominates in the community. On this note, future works may use such an eco-evolutionary model based on trait-mediated interactions to investigate on the response of mutualistic communities to biological invasion for a broader scope of invader characteristics.

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Supplementary materials

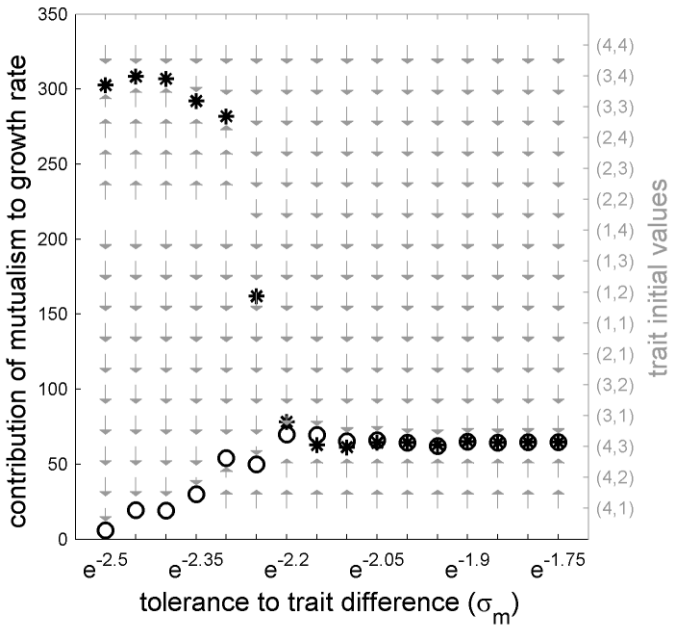

Figure S1: Change in the average over all morphs of the contribution of mutualism to growth rate as a function of the level of tolerance trait difference in mutualistic interactions. Empty circles represent the values when the system evolves towards prioritizing resource accessibility and stars represent the values when the system evolves towards prioritizing mutualistic benefits. Grey arrows indicate the direction of the selection for different initial trait values indicated on the right axis.

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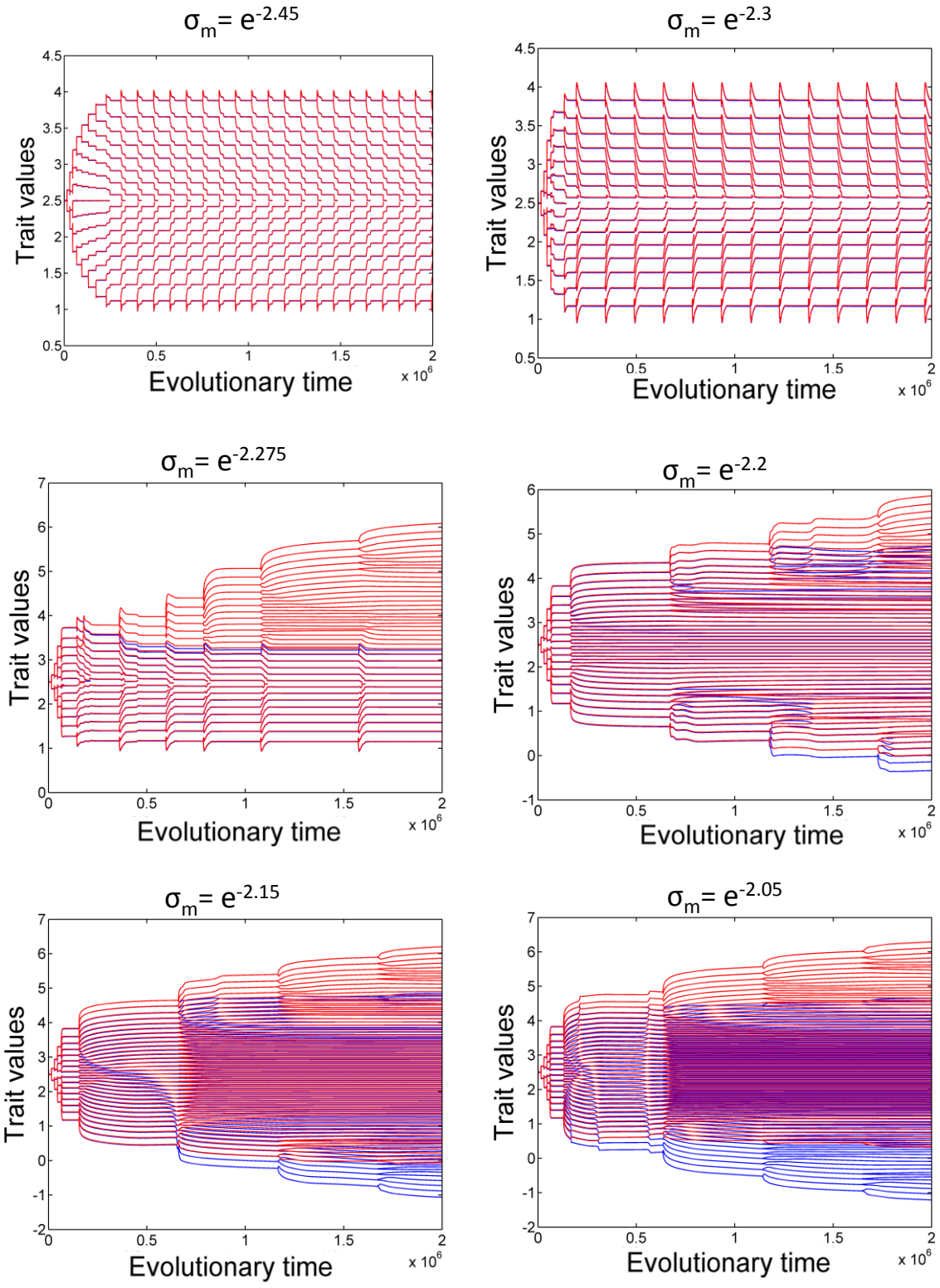

Figure S2: Changes in evolutionary trajectories as the level of tolerance to trait difference (σ_m) is increasing when the morphs start to prioritize for mutualistic benefit.

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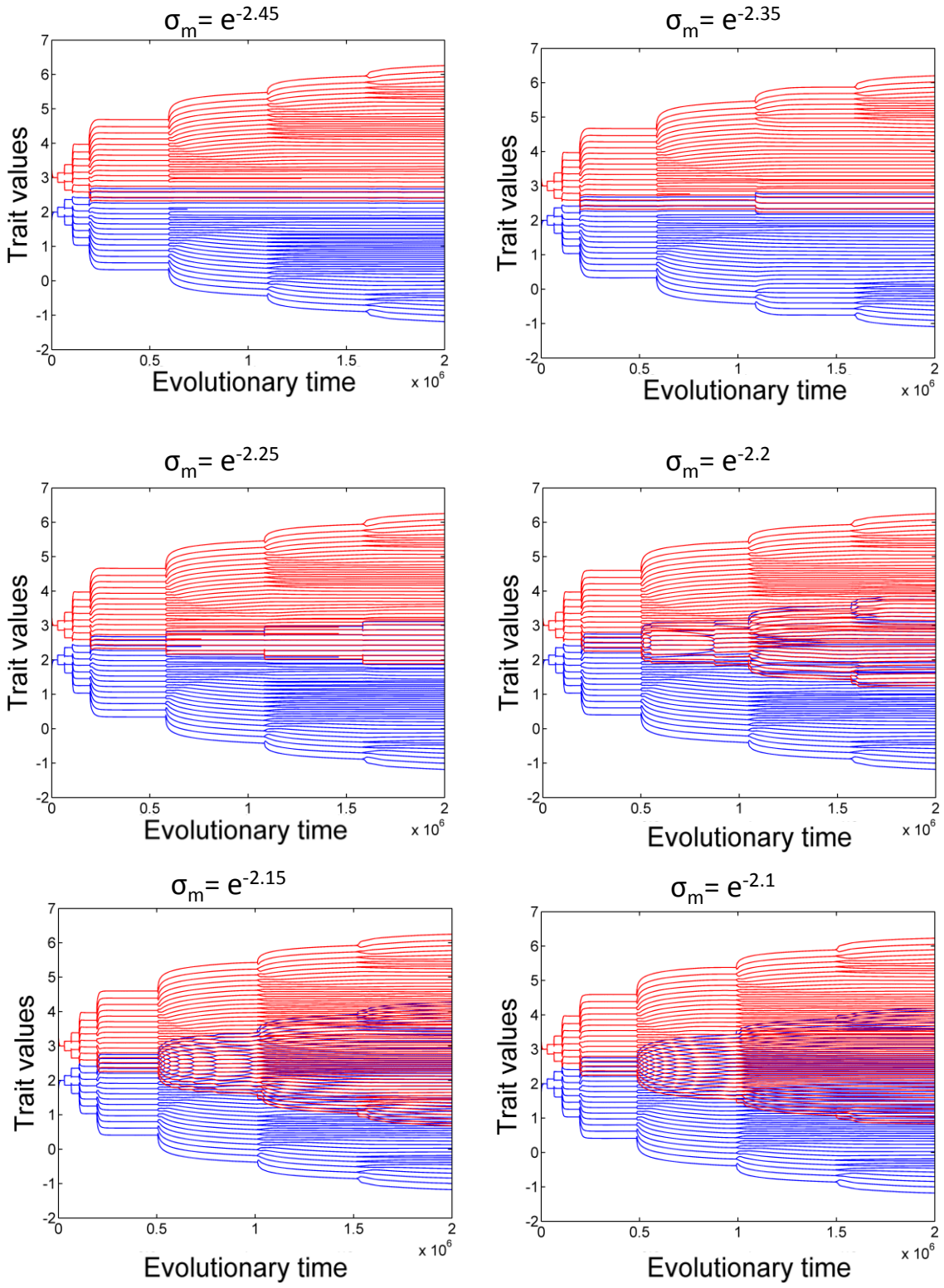

Figure S3: Changes in evolutionary trajectories as the level of tolerance to trait difference (σ_m) is increasing when the morphs start to prioritize resource accessibility.

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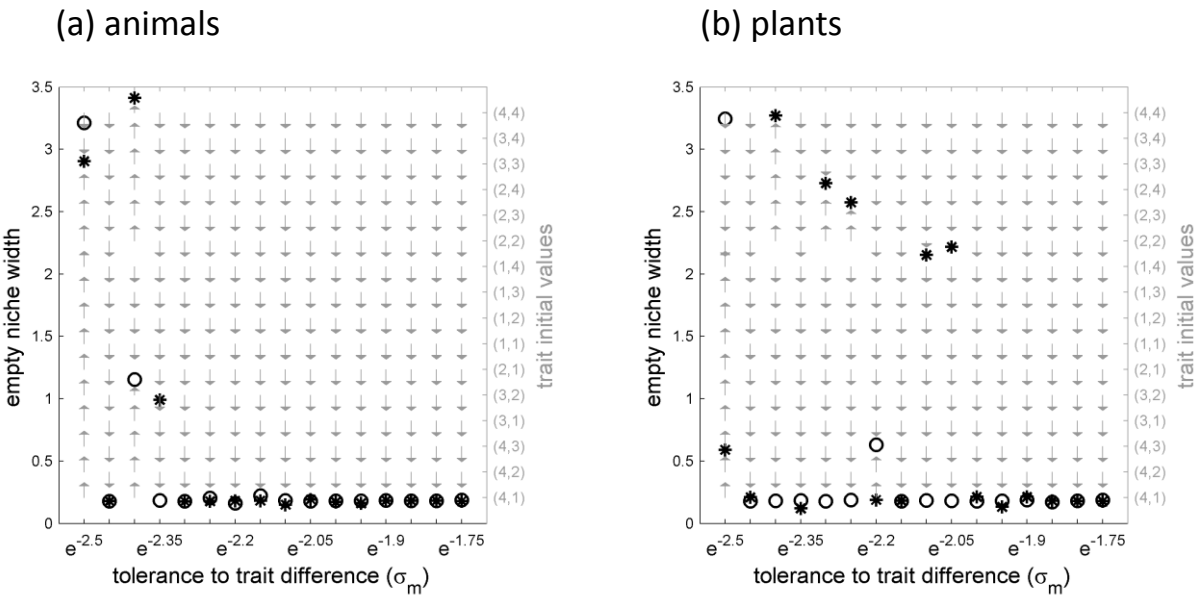

Figure S4: Change in the width of empty exploitable niche (being the maximum over all morphs of the smallest trait difference) as a function of the level of tolerance to trait difference in mutualistic interactions in (a) animal and (b) plant trait space. Empty circles represent the values when the system evolves towards prioritizing resource accessibility and stars represent the values when the system evolves towards prioritizing mutualistic benefits. Grey arrows indicate the direction of the selection for different initial trait values indicated on the right axis.

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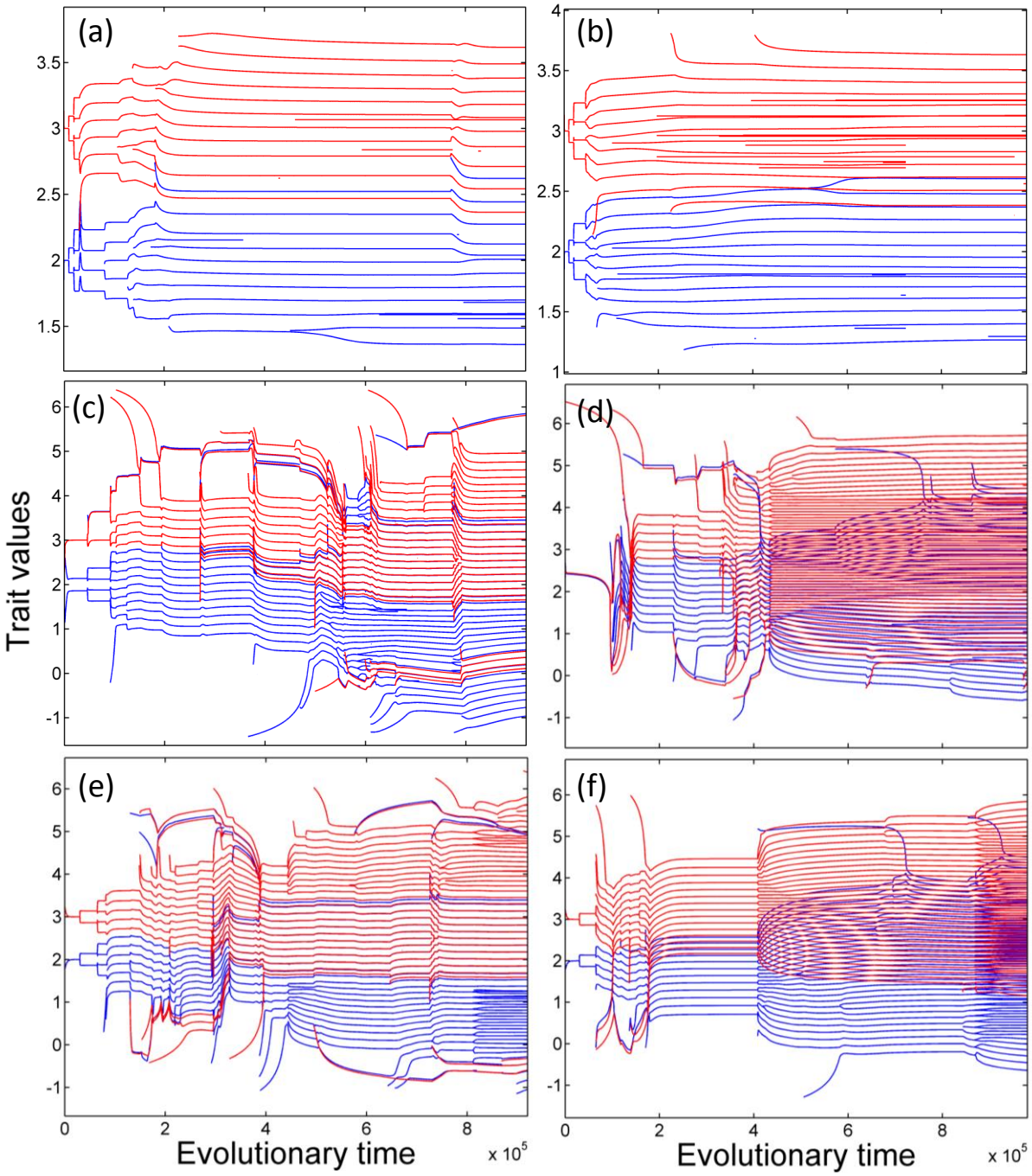

Figure S5: Evolution of trait values for different evolutionary trajectories with introduction of alien morphs into the system. Animal trait values are in red while plant trait values are in blue. Alien morphs are drawn uniformly from the viable niche space of the native morphs and introduced into the system at a rate of 0.01. Parameters are as in Fig.2.

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CHAPTER 4

Trait-mediated interaction leads to structural emergence in mutualistic networks

"Bottomless wonders spring from simple rules, repeated without end."

Benoit Mandelbrot

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ORIGINAL PAPER

Trait-mediated interaction leads to structural emergence in mutualistic networks

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Abstract As asymmetric structures of mutualistic networks can potentially contribute to system resilience, elucidating drivers behind the emergence of particular network architectures remains a major endeavour in ecology. Here, using an eco-evolutionary model for bipartite mutualistic networks with trait-mediated interactions, we explore how particular levels of connectance, nestedness and modularity are affected by three network assembly forces: resource accessibility, tolerance to trait difference between mutualistic pairs and competition intensity. We found that a moderate accessibility to intra-trophic resources and cross-trophic mutualistic support can result in a highly nested web, while low tolerance to trait difference between interacting pairs leads to a high level of modularity. Network-level trait complementarity leads to low connectance and high modularity, while network-level specialization can result in nested structures. Consequently, we argue that the interplay of ecological and evolutionary processes through trait-mediated interactions can explain these widely observed architectures in mutualistic networks.

Keywords Network architecture · Nestedness · Connectance · Compartmentalization · Modularity · Trait complementarity · Network specialization

Electronic supplementary material The online version of this article (doi:10.1007/s10682-015-9798-z) contains supplementary material, which is available to authorized users.

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Introduction

Mutualistic networks are formed by interactions between species who exploit each other for mutual benefit, such as the interactions between flowering plants and their pollinators and between many plants and their seed dispersers. Despite their diversity, mutualistic interactions exhibit surprisingly well-organized structures (Bascompte and Jordano 2007). In particular, they are often found to be within a certain range of connectance, nestedness and modularity (Bascompte and Jordano 2007; Jordano et al. 2003; Vazquèz and Aizen 2004). Connectance measures the proportion of realized interactions among all possible ones in a network, and mutualistic networks often have a low to moderate level of connectance (Olesen and Jordano 2002). A high level of nestedness, where specialists only interact with a subset of species with which generalists interact (Bascompte et al. 2003), is also a common feature of mutualistic networks (Thébault and Fontaine 2010). Modularity depicts the extent to which a network is compartmentalized into delimited modules where species are strongly interacting with species within the same module but not those from other modules (Olsen et al. 2007). Being a typical feature of food webs (Thébault and Fontaine 2010), high modularity is also common in some mutualistic networks (Olesen et al. 2007; Guimarães et al. 2007; Mello et al. 2011).

Probing mechanisms and processes that drive the emergence of these network structures is essential for safeguarding the ecosystem service provided by mutualistic networks, as network structures can have important roles in network stability and resilience (Bastolla et al. 2009; Thébault and Fontaine 2010). Some studies have hypothesized that network structures are the consequence of neutral processes such as random interactions between species, where the probability of an interaction depends only on the relative abundances of species (Vazquèz 2005; Stang et al. 2006; Vazquèz et al. 2007). In contrast, others have argued that these network structures are a consequence of non-neutral evolutionary and ecological processes (Olsen et al. 2007; Thompson et al. 2013; McQuaid and Britton 2013a; Encinas-Viso et al. 2014; Nuwagaba et al. 2015). For instance, phylogenetic history can partially explain the emergence of particular network structures (Rezende et al. 2007; Minoarivelo et al. 2014; Chamberlain et al. 2014), although the use of phylogeny developed from neutral genetic markers could mask the role of biotic interactions.

The concept of trait-mediated interaction has been a subject of much debate since its inception (Abrams 2007). Although it was originally defined to describe the indirect effect of a mediator species on the interaction between the two mediated species (Abrams et al. 1996), the term has gradually been adopted to describe any dependence of biotic interactions on traits (Bolker et al. 2003; Bolnick and Preisser 2005). While most studies on food webs still use its original meaning (Werner and Peacor 2003), studies on mutualistic interactions have preferred the broader meaning (Guimarães et al. 2011; Nuismer et al. 2010), which is the sense that will be employed in this study. Empirical and theoretical studies have shown that the adaptive response of behavioural and phenotypic traits to biotic interactions can swiftly alter the outcome of these interactions (Werner and Peacor 2003). For instance, differences in particular traits could constrain the possibility of interactions between species pairs, thus posing a threshold on traits for feasible interactions (Snow and Snow 1972; Bascompte et al. 2006; Stang et al. 2006). Such a threshold on traits has been found important for determining the interaction structures of many ecological networks (Stang et al. 2007). Trait-mediated interactions can be much stronger than density-mediated interactions (Wissinger and McGrady 1993; Railsback et al. 1999; Schmitz et al. 2004), especially in some pollination networks where the length distributions of proboscis

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and floral tubes are better predictors of interaction incidence and strength than the relative abundances of species (Stang et al. 2009).

Although the effect of population density on biotic interactions is straightforward through the effected encounter rate, an increasing number of studies have resorted to the importance of behavioural and morphological traits in changing interaction strength and thus network structures. A number of studies have focused on the role of behavioural and morphological traits in shaping network structures (McQuaid and Britton 2013a; Chamberlain et al. 2014; Rafferty and Ives 2013). Biotic interactions could be directly mediated by a linkage rule between interacting traits (Santamaría and Gironés 2007), forming trait complementarity (high degree of trait matching between interacting pairs) and trait convergence (traits within a trophic tend to be more similar than expected) (Guimarães et al. 2011; Nuismer et al. 2012). Following on from these trait-based studies, we consider how interacting traits can potentially affect the emergence of network structures via mediating both the intra-trophic competition and the cross-trophic mutualistic interaction, with the interaction strength a function of the trait matching/difference between interacting species (Nuismer et al. 2010). The level of trait mismatching can be measured as the length difference between proboscis and pollen tube in a typical case of pollination syndrome, whilst as the size difference between the body/jaw and the fruit/seed in the case of frugivores and seed-dispersal networks.

In contrast to typical trait-based approaches, we design an eco-evolutionary model depicting simultaneously the ecological dynamics of population densities happening at a fast time scale and the evolutionary dynamics of interacting traits happening at a slow time scale, using the framework of *adaptive dynamics* (Metz et al. 1992; Dieckmann and Law 1996; Dercole and Rinaldi 2008). By analyzing the structures of resultant networks, we aim to investigate how features of trait-mediated interactions shape the architecture of mutualistic networks. In particular, we explore (1) how the specialization of trait-mediated interactions, including competition, mutualism and resource exploitation, affect the structures of mutualistic networks; (2) how much variation in network structures can be attributed to density-mediated interactions (measured by network size and total abundance) and trait-mediated interactions (measured by trait convergence and complementarity).

Materials and methods

Evolutionary and ecological processes are intertwined. Evolutionary changes in functional traits can affect ecological processes such as the way species interact and subsequently the behaviour of population dynamics/demography. In return, functional traits will change in response to varying frequency-dependent selection from changing population densities. As such, we describe a model of mutualistic network emergence, implementing exactly such interdependence between population dynamics and trait evolution. Specifically, we assume that resource competition becomes intense between two species with similar traits. Moreover, matching traits between a pair of mutualistically interacting animal and plant species confers on them high fitness rewards. Following the framework of adaptive dynamics, traits can evolve disruptively and diversify adaptively into multiple interacting ones, forming an ecological network. Here we focus on how the specialty of trait-mediated interactions, i.e. the level of trait matching in resource competition and mutualistic interactions, affect the architecture of emerged mutualistic networks.

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Eco-evolutionary dynamics

Let there be n functional morphs of animals and m functional morphs of plants. Each functional morph, indexed by i for animals and j for plants, is characterized by its population density A_i (for $i \in 1,\ldots, n$) and P_j (for $j \in 1,\ldots, m$), respectively. We denote the trait of animal morph i by x_i and the trait of plant morph j by y_j. The population dynamics of the system is depicted by a Lotka–Volterra model with a Holling (1959) type II functional response, as in Zhang et al. (2011) and Nuwagaba et al. (2015):

$$\frac{dA_i}{A_i dt} = f_A(x_i) = r_A - \frac{r_A \sum_k \gamma(x_i, x_k) A_k}{K_A(x_i)} + \frac{\sum_j b_{A_i P_j} w_{A_i P_j} P_j}{1 + h \sum_j w_{A_i P_j} P_j}, \tag{1a}$$

$$\frac{dP_j}{P_j dt} = f_P(y_j) = r_P - \frac{r_P \sum_k \gamma(y_j, y_k) P_k}{K_P(y_j)} + \frac{\sum_i b_{P_j A_i} w_{P_j A_i} A_i}{1 + h \sum_i w_{P_j A_i} A_i}, \tag{1b}$$

where r is the intrinsic population growth rate, and h the handling time that animals spend for visiting a plant and digesting the nutrients extracted from the plant; both are assumed to be trait-independent to avoid over-parameterization of the model ($r_A = r_P = 1$; $h = 0.1$). In the following, all terms in Eq. (1b) can be mirrored from the specified formulation in Eq. (1a).

The carrying capacity, K_A and K_P, varies between morphs, representing trait-mediated resource accessibility. Following Doebeli and Dieckmann (2000), we used a Gaussian function for the carrying capacity: $K_A(x_i) = k_A N\left(x_A^{\max}, \sigma_A, x_i\right)$, where k_A (=400) is a scaling constant, and $N\left(x_A^{\max}, \sigma_A, x_i\right)$ the Gaussian density function of trait x_i with the maximum carrying capacity at $x_A^{\max}$ (=3) and the standard deviation σ_A. Similarly, we set the baseline values of k_P (=300) and $y_P^{\max}$ (=2) for the plant species in the following analysis.

The intra-trophic competition function γ is set to let morphs with more similar traits suffer stronger competition. We used a Gaussian function for depicting the competition intensity between morphs (Bürger et al. 2006; Doebeli and Dieckamann 2000; Doebeli and Ispolatov 2011; Raimundo et al. 2014): $\gamma(x_1, x_2) = \exp\left(-(x_1 - x_2)^2 / 2\sigma_C^2\right)$, where σ_C controls the width of the competition kernel. The cross-trophic mutualistic benefit, b_{AP}, reflects the assumption of assortative interactions that matched traits bring to each other high profit, and is also assumed to follow a Gaussian function of trait difference: $b_{AP}(x_i, y_j) = c \cdot \exp\left(-(x_i - y_j)^2 / 2\sigma_m^2\right)$, where c (=0.1) is a parameter controlling the magnitude of the maximum mutualistic support, and the parameter σ_m controls the tolerance level of successful interactions to the dissimilarity of involved traits (Nuismer et al. 2010). The interaction preference of two morphs w_{AP} determines the possibility of interaction after the encounter and is assumed to follow adaptive foraging strategies, depending on both the benefit and abundance of involved morphs (Doebeli and Dieckmann 2000; Zhang and Hui 2014). Modifying the expression which describes the strength of mutualistic support in Doebeli and Dieckmann (2000) and Egas et al. (2005), we have the following function for the adaptive interaction preference: $w_{A_i P_j} = b_{A_i P_j}^{\beta} \Sigma_k A_k / \Sigma_k \left(A_k b_{A_k P_j}\right)^{\beta}$, where β is a parameter that determines whether the interaction is optimal ($\gg 1$), suboptimal (=1) or neutral (=0); the summation term $\Sigma_k A_k$ in the numerator is for normalization. For simplicity yet without losing generality, we chose $\beta = 1$ in the following analyses.

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Functional traits of interacting morphs are subject to mutations. This can also be interpreted as the replacement and reassembling of local species through colonization and invasion of species with novel traits. Mutation normally happens at a low rate so that the populations can be considered at their ecological equilibriums when the mutation occurs (Doebeli and Dieckmann 2000). We only consider the non-trivial strictly positive and asymptotically stable equilibrium points of the system ($\tilde{A}_i(x_i, y_j)$ and $\tilde{P}_j(x_i, y_j)$). When a mutation enters the system, the resident morph and the mutant undergo an intra-trophic competition determined by Eq. (1). Let x_i' and y_j' be the mutant trait of animal morph i and plant morph j, and let $X = (x_1,\ldots, x_n)$ and $Y = (y_1,\ldots, y_m)$ be the trait vectors of the resident morphs. We can define the invasion fitness of the rare mutants at the equilibrium points as their per-capita growth rates when setting their initial densities to be negligible: $f_A(x_i')$ and $f_P(y_j')$. The selection gradient, defined as $g_{A_i} = \partial f_A(x_i')/\partial x_i'|_{x_i'=x_i}$ and $g_{P_j} = \partial f_P(y_j')/\partial y_j'|_{y_j'=y_j}$, determine the direction and speed of trait evolution, and an evolutionary singularity is defined as the traits $(\tilde{x}_i, \tilde{y}_j)$ when the selection gradient disappears. The evolutionary dynamics of the functional traits can be depicted by the canonical equations of adaptive dynamics (Dieckmann and Law 1996):

$$\begin{aligned} dx_i/dt &= m_A \tilde{A}_1 g_{A_i} \\ dy_j/dt &= m_P \tilde{P}_1 g_{P_j} \end{aligned}, \tag{2}$$

where m_A and m_P are parameters proportional to the rate and variation of the mutation (set to 10^{-3}) in the analysis. An evolutionary branching is to occur in the system provided three conditions are satisfied. First, the singularity $(\tilde{x}_i, \tilde{y}_j)$ should be an evolutionary attractor of directional selection; that is, it is convergence stable. This happens when all eigenvalues of the Jacobian matrix of Eq. (2) have negative real parts (see Doebeli and Dieckmann 2000); this means $\partial g_{A_i}/\partial x_i|_{x_i=\tilde{x}_i} < 0$ and $\partial g_{P_j}/\partial y_j|_{y_j=\tilde{y}_j} < 0$. Second, the singularity should represent a fitness minimum to induce disruptive selection and to allow the mutant to invade (Geritz et al. 1998); that is, $\partial^2 f_A/\partial x_i'^2|_{x_i'=\tilde{x}_i} > 0$ and $\partial^2 f_P/\partial y_j'^2|_{y_j'=\tilde{y}_j} > 0$. Finally, the mutant and the resident morphs need to coexist to ensure the protection of dimorphism from the evolutionary branching (Geritz et al. 1998); that is, the two morphs can invade each other: $(\partial^2 f_A/\partial x_i^2 + \partial^2 f_A/\partial x_i'^2)|_{x_i'=x_i=\tilde{x}} > 0$ and $(\partial^2 f_P/\partial y_j^2 + \partial^2 f_P/\partial y_j'^2)|_{y_j'=y_j=\tilde{y}_j} > 0$.

Numerical simulation

We numerically solved the population dynamics (Eq. 1) and the canonical equations of adaptive dynamics (Eq. 2), with an initial population density of 1 for both plants and animals (unless otherwise specified), and set the initial trait values to be different (2.25 for animals and 2.75 for plants). Note that, the dynamics of trait evolution is independent of the initial conditions as the system will converge to the same evolutionary singularity (Fig.S1). Following Doebeli and Dieckmann (2000), we only chose the aforementioned initial values for illustration, which can take any real numbers nonetheless. It is worth noting that, although the trait of a species can take any values (e.g. log-transformed body size as a focal trait can range from negative to positive infinity, theoretically speaking), only those that are feasible and can ensure its own viability, i.e. with a positive equilibrium in Eq. (1), can be realised in the model. Once the system reaches its singularity, the three conditions for evolutionary branching will be examined. If satisfied, a new morph will be

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added to the system with its trait value slightly different from the resident trait (+0.01) and having a low initial density (10 % of its resident population density). The density of the resident morph will be simultaneously updated to be 90 % of its original. The process was repeated until the system reached its evolutionarily stable strategy (ESS). Not all observed ecological systems, as an ongoing evolving identity, have reached an ESS due to insufficient establishment duration and perturbations. For such cases where the system has an ESS but took too much computational time to reach some of its singularities, we stopped the simulation at 10^7 evolutionary time steps. Note that there were cases where the system did not have an ESS (e.g. the case of Red Queen dynamics); we stopped the simulation after the system has reached its singularity repeatedly eight consecutive times.

We focused on the effects of three key parameters on the evolutionary dynamics, including the width of the intra-trophic competition kernel (σ_C), the tolerance to trait difference in a mutualistic interaction (σ_m) and the width of resources accessibility (σ_A for animals and σ_P for plants; we keep $\sigma_A = \sigma_P$ for simplicity). A wide competition kernel (large σ_C) indicates a low sensitivity of intra-specific competition to trait difference; that is, a species of such can compete with a wide range of species for resources. Low tolerance to trait difference (small σ_m) suggests that mutualistic benefits can only be assured by interacting with mutualistic partners with closely similar traits. Higher resource

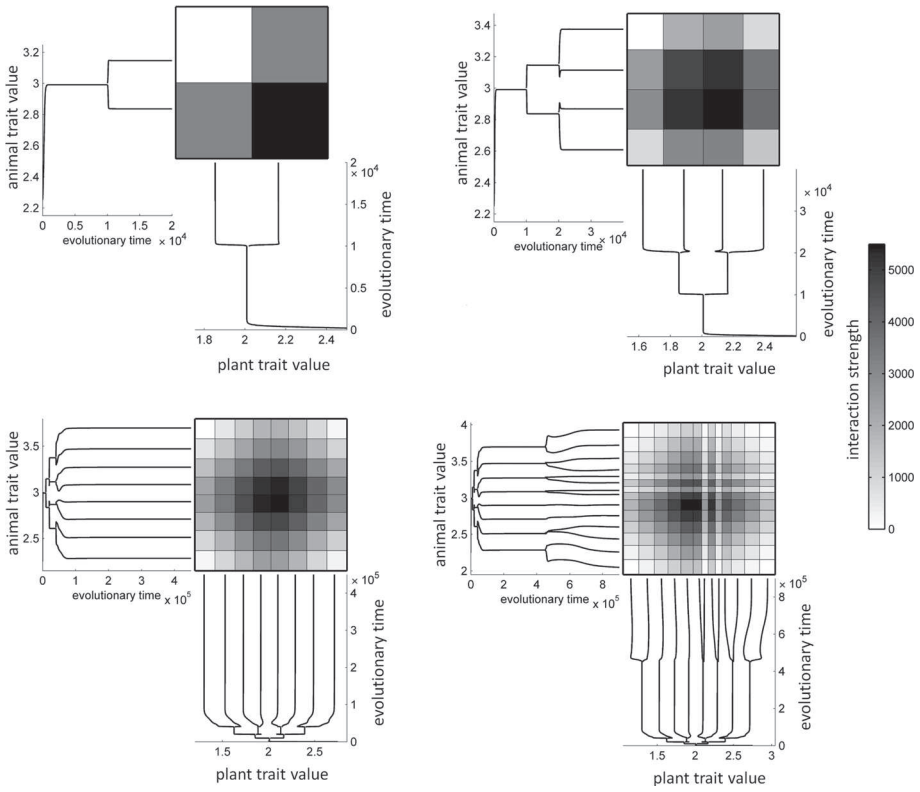

Fig. 1 The evolutionary dynamics (four snapshots) of a bipartite mutualistic network, represented as the evolutionary trees of interacting traits and the interaction strength matrix. Parameters: $\sigma_A = e^{-1}$, $\sigma_c = e^{-2}$, $\sigma_m = e$

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accessibility (large σ_A) indicates a wider exploitable niche space (Fig.S2). We simulated the evolutionary dynamics for all combinations of σ_A, σ_C and σ_m, ranging from e^{-3} (≈ 0.05) to e, with a multiplicative step of $e^{1/4}$; a total of 4913 ($=17^3$) runs. We ran additional parameter sensitivity tests on model behaviours, showing consistent and robust results (Fig.S3 and Fig.S4).

Network analysis

We considered the bipartite mutualistic networks formed by interactions between the two sets of animal morphs and plant morphs produced at the end of each simulation. Cases where the system gave no evolutionary branching (monomorphic systems) were discarded from the study as they cannot be considered as a network. Although mutualistic interactions are typically recorded in a binary format, quantitative datasets can be more informative, especially with the potential of incorporating information on interaction strength (McQuaid and Britton 2013a; Schleuning et al. 2014). Here, we depicted the network as a quantitative interaction matrix (Q) where its elements (q_{ij}) represent the interaction strength between animal i and plant j. Following Berlow et al. (2004), we define the interaction strength as the non-linear functional response term of Eq. (1), depending on both the number of recruited animals i from interacting with animals j, and the number of recruited plants j from interacting with animals i, per time unit:

$$q_{ij} = \frac{1}{2}\left(\frac{A_i b_{A_i P_j} w_{A_i P_j} P_j}{1 + h w_{A_i P_j} P_j} + \frac{P_j b_{P_j A_i} w_{P_j A_i} A_i}{1 + h w_{P_j A_i} A_i}\right). \quad (3)$$

When the element q_{ij} is $<10^{-8}$, it was considered to be equal to zero, indicating a negligible interaction. An illustration of trait evolution in an ecological network, depicted as evolutionary trees and interaction matrices, is provided in Fig. 1.

We considered the following metrics for quantitative networks. First, the quantitative connectance metric was computed as the quantitative linkage density divided by the number of species in the network (Tylianakis et al. 2007). Second, we used the metric WNODF (Weighted Nestedness metric based on Overlap and Decreasing fill) for depicting the level of nestedness (Almeida-Neto and Ulrich 2011). Finally, the level of modularity was measured using a new algorithm *QuanBimo* (Dormann and Strauβ 2014; adapted from Claused et al. 2008). All these network metric measurements are implemented in the R library *bipartite* (Dormann et al. 2008).

To further investigate the possible causes of network structure, a few additional network-level metrics were computed. First, the level of specialization of each network was measured according to the quantitative index H_2' of Blüthgen et al. (2006), implemented in the R library *bipartite* (Dormann et al. 2008). This index measures the overall deviation of species' realized degrees from their expected ones, ranging from 0 (no specialization) to 1 (perfect specialization). Second, to quantify the level of trait divergence in each trophic (animal or plant), we used the functional trait dispersion index *FDis* (Laliberté and Legendre 2010). It depicts the mean distance of individual species trait to the centroid of all species traits, weighted by population abundance of each species, ranging from 0 (no dispersion) to 1 (highly dispersed), implemented in the R library *FD* (Laliberté et al. 2014). Third, we measured the trait complementarity between animals and plants after modifying Guimarães et al.'s (Guimarães et al. 2011) metric to incorporate the effect of interaction strength, $Cp = -\ln D$, where $D = (\Sigma_i \Sigma_j D_{ij})/(n \times m)$ is the average phenotypic trait

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difference between interacting pairs, weighted by the normalized interaction strength, $D_{ij} = |x_i - y_j| \times \bar{q}_{ij}$. Finally, network size (N) was measured as the total number of animal and plant morphs at the end of the simulation.

We tested the effect of network size (N), total abundance (Ab), level of trait complementarity (Cp), animal and plant functional trait dispersion ($FDis_{an}$ *and* $FDis_{pl}$) on network structures (connectance, nestedness and modularity) using a linear regression. Before the linear regression, we assessed the mutlicollinearity of these explanatory variables using the variance inflation factor (VIF), implemented in the R library *fmsb* (Nakazawa 2014). The variable with the highest VIF score was first removed, and then a new VIF analysis was performed until all the VIF scores of the remaining variables were below five. These selected variables were then used in the linear regression. We estimated the contribution of a particular variable to explaining the variation of network structures as the reduction of adjusted R^2 after removing the variable.

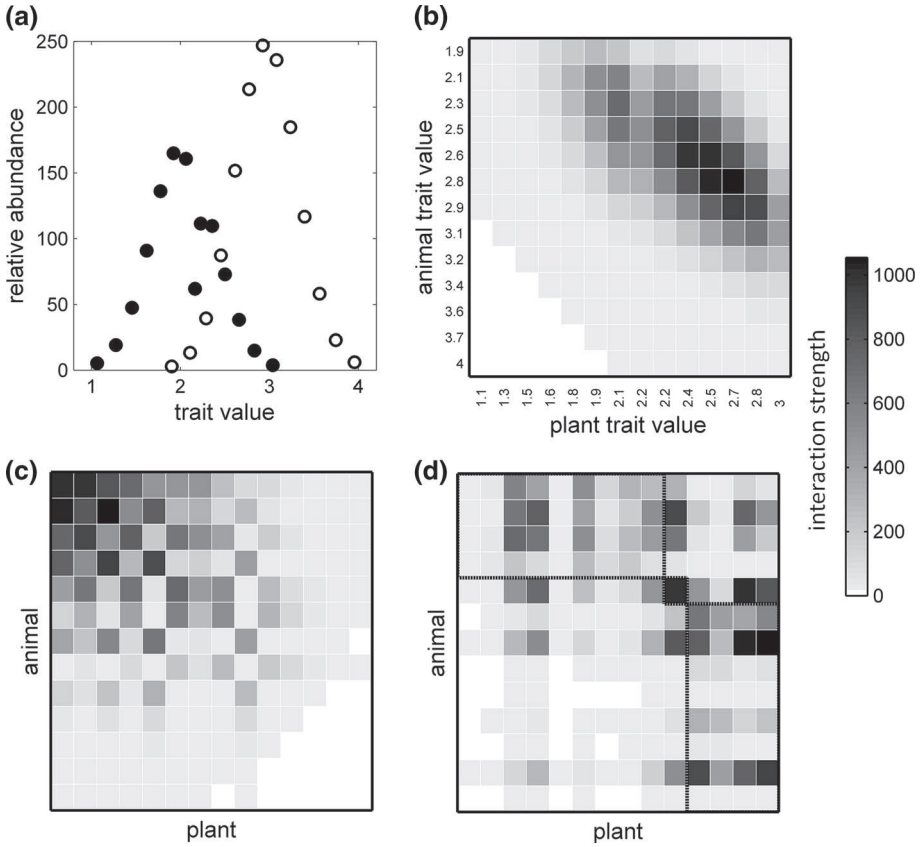

Fig. 2 An example of a mutualistic network produced from the model. **a** Relationships between trait values and their corresponding population abundance of animals (*open circles*) and plants (*closed circles*). **b** The weighted matrix of interaction strength, with *rows* and *columns* sorted according to trait values. **c** *Rows* and *columns* are sorted to show the pattern of nestedness (WNODF = 0.58). **d** *Rows* and *columns* are sorted to show the pattern of modularity (Mod = 0.23). Parameters: $\sigma_A = e^{-1}$, $\sigma_c = e^{-2}$, $\sigma_m = e^{-1}$

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Results

Network structure emergence

The model can produce mutualistic networks with structures comparable to real networks (see Fig. 2 for an illustration of patterns on relative abundance and interaction matrices sorted for traits, nestedness and modularity). For all tested parameter values, connectance ranged from 0.015 to 0.5 with an average of 0.26 ± 0.14 (mean ± standard deviation; in the same format hereafter), with highly connected networks emerging when the resource accessibility is narrow (small σ_A) and the tolerance to trait difference is high (large σ_m) but insensitive to the change of intra-trophic competition kernel (σ_C) (Fig. 3 first column). Nestedness ranged from 0 (no pattern of nestedness) to 1 (perfectly nested), with an

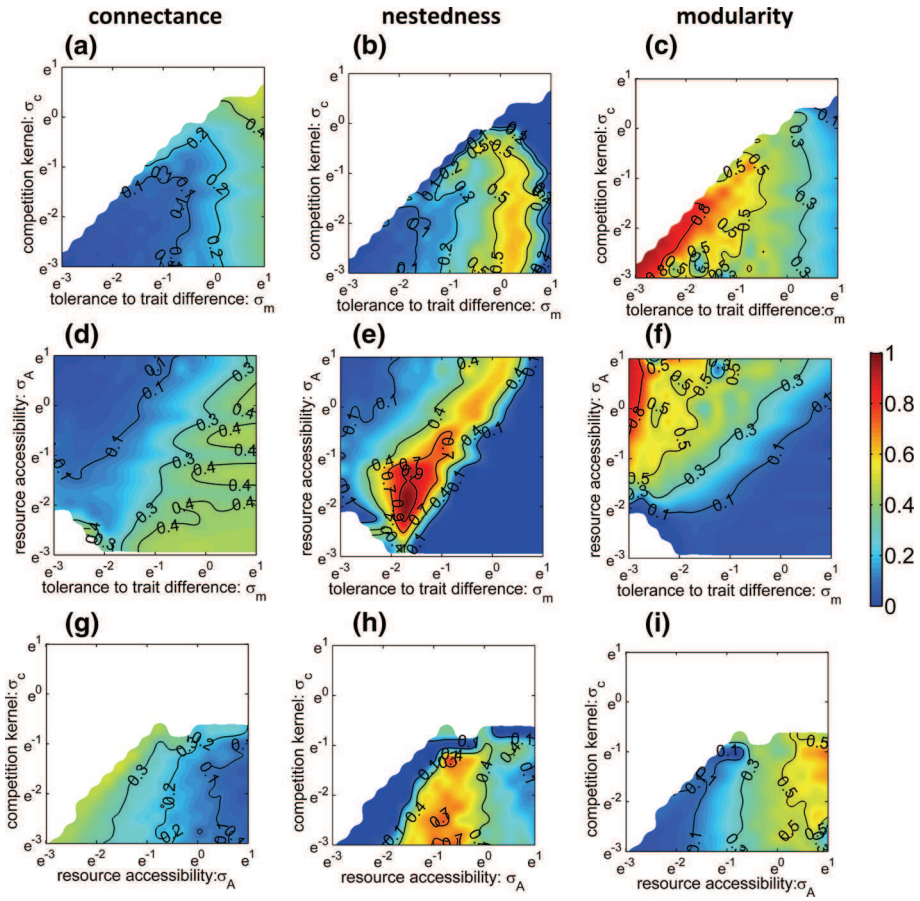

Fig. 3 The quantitative connectance (*first column*), weighted nestedness (*second column*) and quantitative modularity (*third column*) of emerged networks as a function of model parameters (σ_A, σ_c and σ_m). Specifically, in each plot we varied two parameters and kept the third parameter fixed. The fixed parameters are $\sigma_A = e^{0.75}$ for the *first row*, $\sigma_c = e^{-3}$ for the *second row*, and $\sigma_m = e^{-1}$ for the *third row*, respectively. The *white* area in each plot represents unfeasible parameter zone where the system becomes monomorphic with no network metrics calculated

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average of 0.22 ± 0.25; highly nested networks emerged when the resource accessibility (σ_A) and the tolerance to trait difference (σ_m) were moderate but with a narrow competition kernel (small σ_C) (Fig. 3 second column). Modularity ranged from 0 (no signal of compartmentalization) to 0.96 (highly compartmentalized networks) with an average of 0.28 ± 0.22, with highly compartmentalized networks emerging when the resource accessibility is high (large σ_A), the intra-trophic competition kernel low or moderate (σ_C), and the tolerance to trait difference low (small σ_m) (Fig. 3 third column). Model parameters and metrics for all simulated networks were given in Table S1.

As the level of nestedness is, by definition, related to how generalists and specialists interact with each other, we further examined the specialization level $\left(H_2'\right)$ of each network. The level of specialization increased slightly with increase in the intra-trophic resource accessibility (σ_A) but decreased notably with increase in tolerance to trait difference (σ_m) (see the color patterns of Fig. 4). High resource accessibility made cross-trophic interaction redundant and thus reduced the potential of the emergence of highly structured networks (Fig. 4a). Low tolerance to trait difference facilitated reciprocal specialization and broke down nested structures (Fig. 4b). In contrast, generalists prevailed when the tolerance to trait difference is high, thus also breaking down the highly nested structures (Fig. 4b). Only a moderate level of specialization can foster high nestedness, which can be achieved through a moderate level of resource accessibility and tolerance to trait difference.

Network variation explained

Two variables were removed from the linear regression based on the VIF analysis: animal functional trait dispersion ($FDis_{an}$) and total abundance (Ab). $FDis_{pl}$ was found to be strongly positively correlated with plant trait dispersion, while (Ab) was positively correlated with network size (Fig.S5). All three remaining explanatory variables (N, Cp,

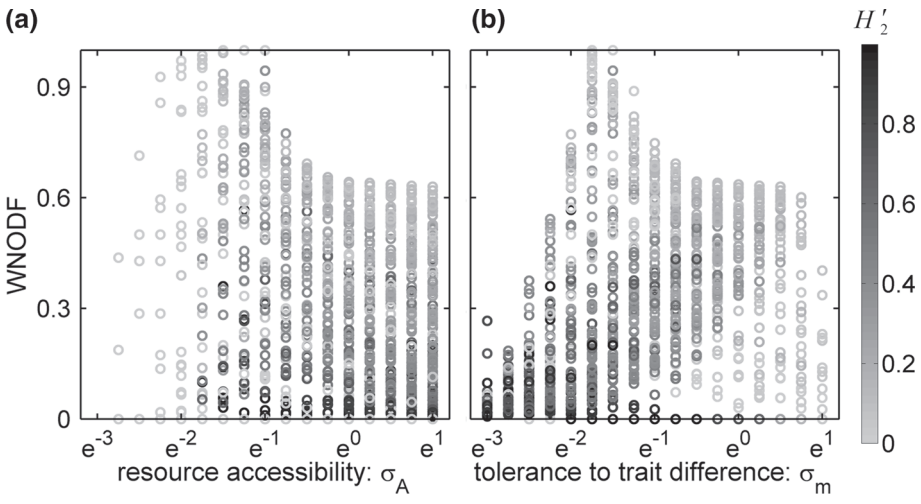

Fig. 4 Weighted nestedness degree of the simulated networks with respect to resource accessibility and the tolerance to trait difference. The *gray* level of each point, representing one network, is the level of specialization (H_2' index). See Table S1 for details

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$FDis_{pl}$) had a significant effect on network structure, except for the trait dispersion on connectance (Table 1). A large portion of variation of connectance (83 %) and modularity (72 %) were explained, although only 11 % variation of nestedness was explained by these three variables.

The explained variation of network connectance dropped drastically when trait complementarity (*Cp*) was removed from the linear regression (Table 1), suggesting it to be the most important constraint to high connectance (Fig. 5). Trait dispersion ($FDis_{pl}$) and network size (*N*) contributed trivially to the variation of network connectance (Table 1). The small percentage of nestedness variation explained (11 %) was mostly due to the contribution of trait complementarity and trait dispersion (Table 1). Network modularity was mostly affected by trait complementarity, followed by trait dispersion, with the contribution from network size negligible (Table 1), suggesting that an increase in trait complementarity and trait dispersion could enhance network compartmentalization (Fig. 5). Modules were largely formed by species with similar traits (due to trait complementarity); however, species with asymmetric traits can also form modules, especially when trait dispersion was driving the emergence of compartmentalization (Fig.S6). The connectance, nestedness and modularity of simulated networks formed an interesting hook shaped relationship in the 3-dimentional space (Fig. 6).

Discussion

By allowing both population density and interacting traits to change, we have made the mutualistic network adaptive at the network assemblage level. The model generated networks comparable to those reported in literature. Our estimates of quantitative connectance (0.26 ± 0.14) are higher than those observed empirically from qualitative networks with binary interaction strength matrices, with a mean of 0.11 in Olesen and Jordano (2002), 0.18 ± 0.15 in Rezende et al. (2007). The connectance decreases with network size following a power law (Fig.S7), consistent with the result from Rezende et al. (2007) (see also the appendix in Suweis et al. 2013). Our average estimate of nestedness (0.22 ± 0.25) is lower than the one from empirical networks (0.37 ± 0.18; Rezende et al. 2007; Minoarivelo et al. 2014). Such discrepancies could be due to that we used interaction

Table 1 Linear regression of connectance, nestedness and modularity on network size (*N*), trait complementarity (*Cp*) and plant trait functional dispersion ($FDis_{pl}$)

	Connectance	Nestedness	Modularity
N	−0.032	0.035	-2.56×10^{-4}
Cp	−0.116	0.066	0.073
$Fdis_{pl}$	−0.001 ^{ns}	−0.059	0.667
Full model	0.83	0.11	0.72
$Cp + FDis_{pl}$	0.77	0.09	0.71
$N + FDis_{pl}$	0.19	0.04	0.32
$N + Cp$	0.82	0.05	0.63

The first horizontal panel shows the regression coefficients for each variable (*ns* non-significant; all the rest are significant with $p < 0.001$); the second panel shows the adjusted R^2 for the full model and reduced models (after removing one variable)

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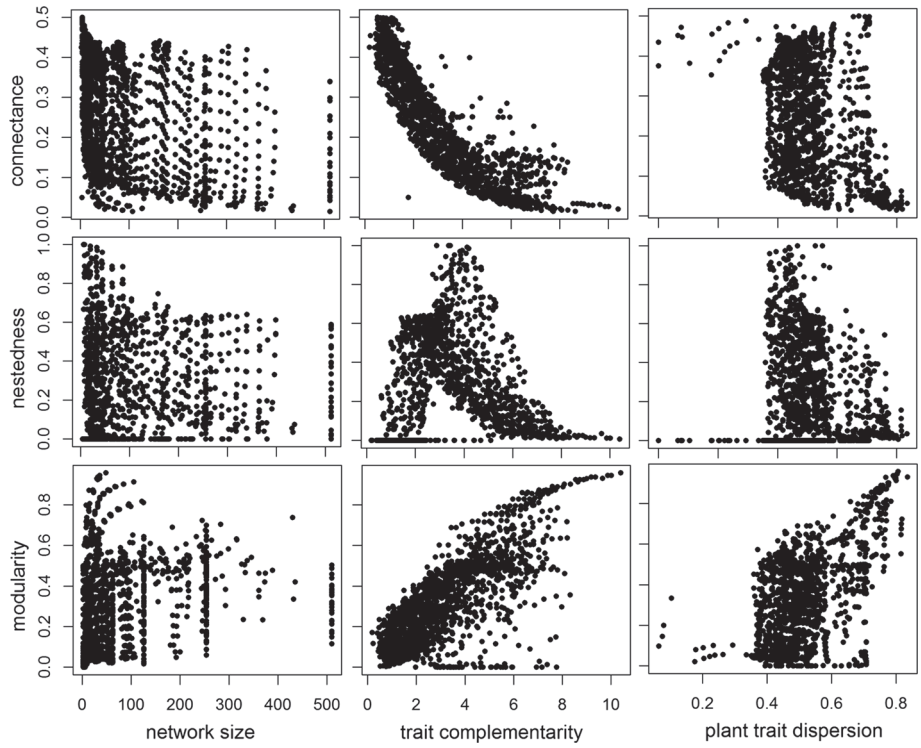

Fig. 5 Relationships between network structures (connectance, nestedness and modularity) and explanatory variables (network size, trait complementarity, plant trait dispersion). See Table S1 for details

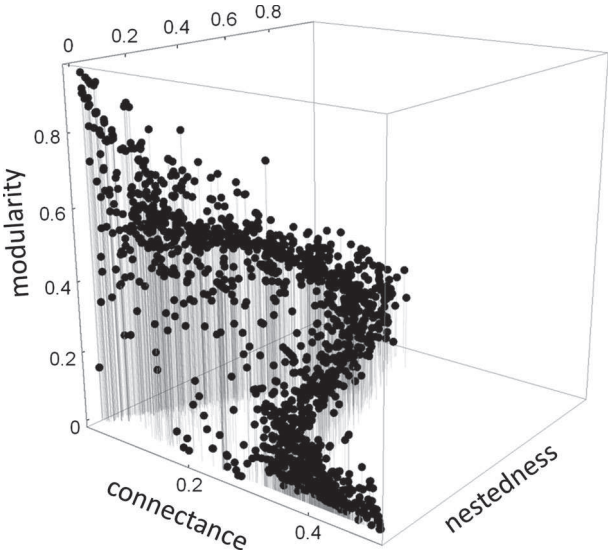

Fig. 6 Relationships between connectance, nestedness and modularity for simulated networks. See Table S1 for details

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strength matrices, rather than binary incidence matrices as used in the mentioned literature. As such, our matrices are less likely to contain zero entries, with many networks fully connected. Networks with no zero entries are automatically scored zero for nestedness, potentially skewed our estimates of connectance and nestedness. In contrast, as algorithms for estimating modularity are designed for considering weighted networks (Schelling and Hui 2015), the estimates of modularity (0.28 ± 0.22) fit well with the observed ones from empirical mutualistic networks (0.27 ± 0.09; Rezende et al. 2007; Minoarivelo et al. 2014).

Nuismer et al. (2012) have suggested that trait-mediated interaction could lead to anti-nested structures in networks due to strong reciprocal specialization. This happens in our system when the tolerance to trait difference (σ_m) is low as species become selective when choosing their mutualistic partners, leading to a high level of specialization and thus a low level of nestedness (Fig. 3). However, when mutualistic benefit (b_{AP}) and resource exploitation (K_A and K_P) contribute comparably to the fitness, the network could become highly nested; this can be achieved at a moderate level of interaction specialization. Adding to McQuaid and Britton's (2013a) conclusion that nested networks can emerge from trait evolution under trade-offs on exploiting mutualistic benefits, we here further showed that the accessibility to both the mutualistic benefit (i.e., the tolerance to trait difference σ_m) and the intra-trophic resources (σ_A) can affect the way species interact and thus shape nested structures.

Empirical mutualistic networks can be highly compartmentalized (Guimarães et al. 2007; Olsen et al. 2007; Donatti et al. 2011; Mello et al. 2011); this happens in our system when the intra-trophic resource accessibility (σ_A) is high and the tolerance to trait difference (σ_m) is low. Parameters for high modularity are not compatible with those for high nestedness, consistent with the result from Fortuna et al. (2010), showing a changing sign of correlation between nestedness and modularity when changing the level of connectance (Fig. 6). Moreover, our finding that interaction modules are largely formed by species with similar traits (Fig.S6) is consistent with the conclusion of Fort and Mungan (2015) on a Mediterranean plant–pollinator network (Stang et al. 2007). By classifying pairs of plants and pollinators into modules based on matching their traits, Fort and Mungan (2015) were able to accurately predict plant and pollinator abundances. As modularity was best explained by trait complementarity (Table 1), drivers of trait complementarity, arising either through coevolution (Olesen et al. 2007; Rezende et al. 2007; Minoarivelo et al. 2014) or adaptive rewiring (Zhang et al. 2011; Schleuning et al. 2014; Nuwagaba et al. 2015), could play crucial roles in the process of network compartmentalization (Donatti et al. 2011; Chamberlain et al. 2014).

Cross-trophic exploitation of resources and mutualistic benefits affected network structures, while intra-trophic competition had a trivial effect on the emergence of asymmetric network structures. This could be because cross-trophic interactions directly affect interaction strength (Eq. 3), while intra-trophic competition only indirectly affects interaction strength through its influence on population size. To this end, competition might not be a driver of the emergence of asymmetric network structures (Bastolla et al. 2009; Encinas-Viso et al. 2012), but only a force of community assembly process.

Trait-mediated direct interactions are apparent in our system (mutualistic interactions and intra-trophic competition), while trait-mediated indirect interactions do also exist here (Peacor and Werner 1997). Indeed, a species can indirectly affect the competition strength between its mutualistic partners. The two mediated species face a trade-off during trait evolution, between targeting mutualistic benefit and resource accessibility, similar to a well-studied model depicting two predators competing for one prey (Werner and Peacor

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2003; Mowles et al. 2011). Phenotypic adaptation of the mediator species induced by one predator can either hamper or improve the foraging efficiency of the other predator (Werner and Peacor 2003). In our case, the mediator species changes its trait to become more similar to its mutualistic partners for maximizing mutualistic benefit. However, if the intra-specific competition kernel (σ_C) is large, two competing species tend to diverge their traits to avoid competition, and the trait of the mediator species will follow the trait of one mutualistic partner. The effectiveness of the other competitor is diminished as a result. However, when σ_C is small, traits of the two competing species are close to each other. Both species can thus explore the mutualistic benefits, and consequently mutualism is facilitated. As a narrow intra-specific kernel (σ_C) corresponds to a high level of nestedness (the case for many empirical mutualistic networks), our study confirms that mutualistic interactions can be a facilitator to competition (Bastolla et al. 2009).

Certainly, using a specific trait to build potential networks could over-simplify the reality. Empirical studies usually make use of a number of functional and behavioral traits judged to be important in structuring the networks (Chamberlain et al. 2010, 2014; Donatti et al. 2011). However, using a single trait to construct potential interaction networks could be simplistic as species with mismatched traits can be part of the same module (Fig.S6). Proposing a multi-dimensional trait space could bring more realism to trait-based network analysis.

Although we here only investigated the structural emergence of mutualistic networks, the model can be opted for antagonistic networks and food webs. Some studies have already appreciated the importance of the linkage between ecological and evolutionary processes for understanding the emergence of complex but realistic food webs (Loeuille and Loreau 2005; Ito and Ikegami 2006; Brännströms et al. 2011). However, the eco-evolutionary approach of network emergence is rarely used for studying antagonistic networks and would certainly deserve more attention. In particular, the host-parasite network model by McQuaid and Britton (2013b) can be considered a good start along this research direction, showing the emergence of nestedness from the evolution of trait-mediated interactions. The appreciation of eco-evolutionary feedbacks in methods of adaptive dynamics and other continuous-trait evolutionary game theory could help to unveil the role of evolutionary processes in the formation of community assemblages and ecological networks (Hui et al. 2015), which are considered in the mainstream through only environmental filtering and biotic interactions.

We assumed that all the morphs are the results of diversification and evolved together under the same environmental conditions (Rezende et al. 2007; Minoarivelo et al. 2014). This contrasts the studies which emphasize the roles of environmental forces, species invasion/colonization and adaptive species rewiring in network emergence (Zhang et al. 2011; Nuwagaba et al. 2015). The fact that a combination of ecological and evolutionary factors explained poorly the nestedness pattern may reveal that some network assemblages can be strongly influenced by external environmental factors such as climate variability (Dalsgaard et al. 2013; Hui et al. 2013; Boyero et al. 2015; Welti and Joern 2015), rather than population demography and life-history traits. On this note, future trait-based network models could encompass these other forces that effect network assemblies (Stouffer et al. 2014; Campbell et al. 2015).

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Supplementary materials

Table S1: Model parameters and network metrics: available at static-content.springer.com/esm/art%3A10.1007%2Fs10682-015-9798-z/MediaObjects/10682_2015_9798_MOESM2_ESM.xlsx

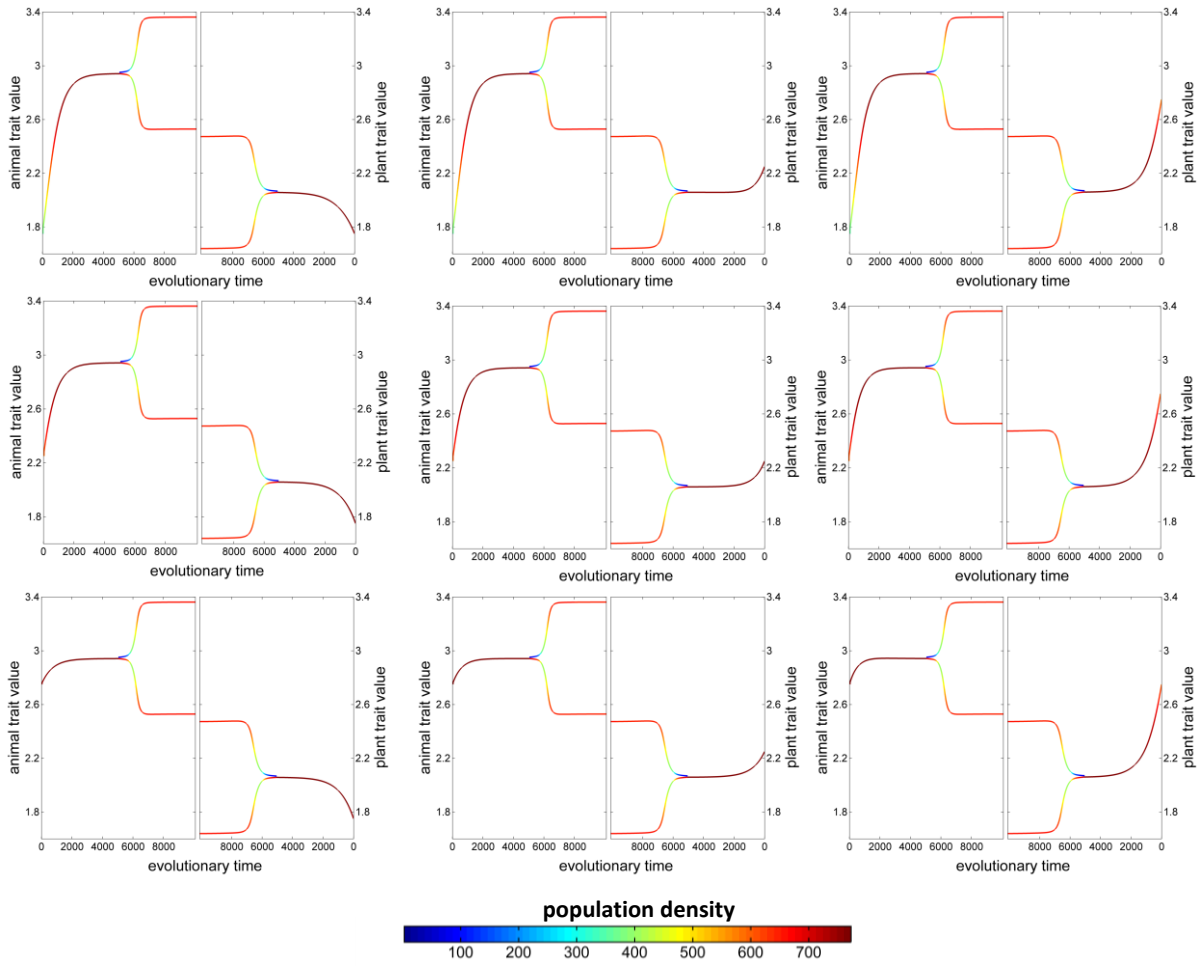

Figure S1: The dynamics of trait evolution under different initial conditions

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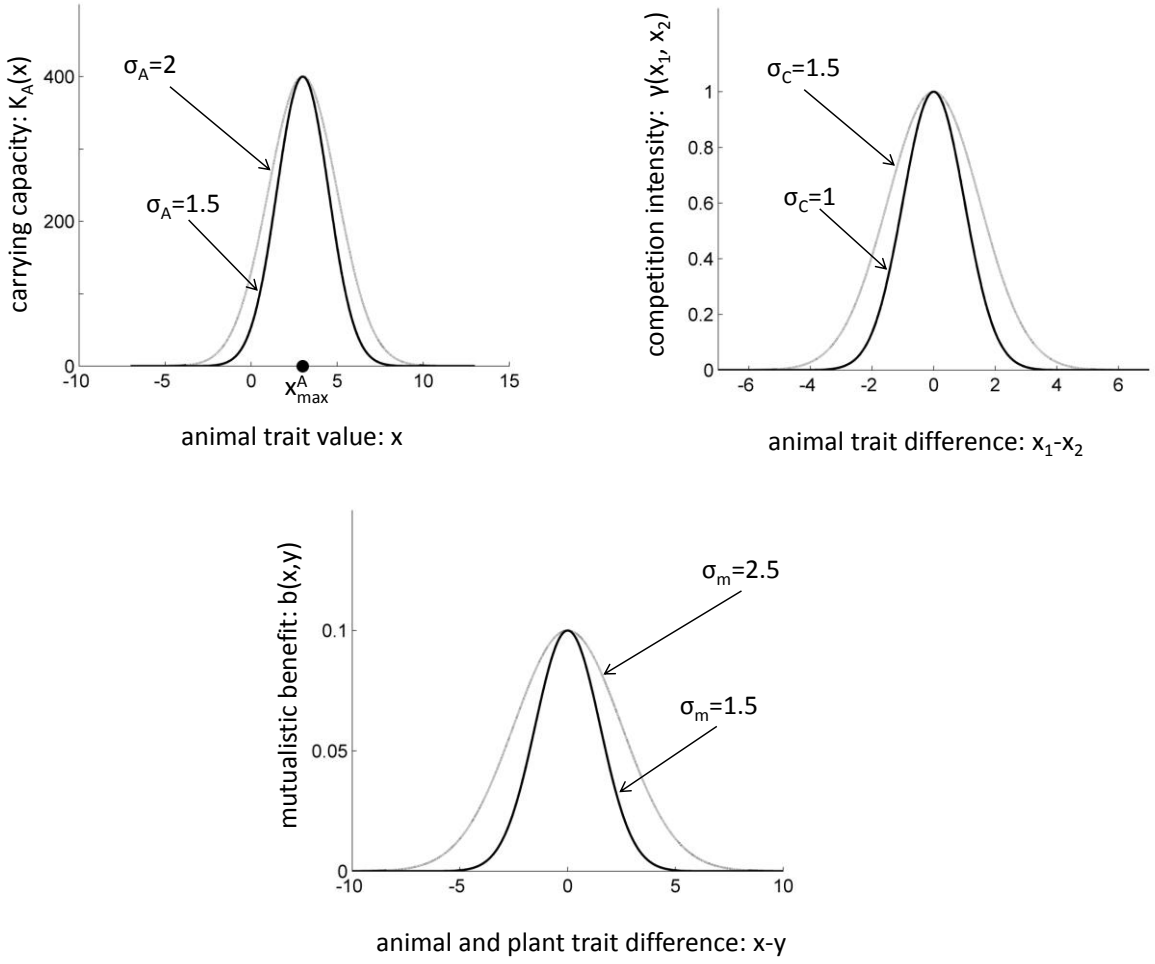

Figure S2: Effects of kernel width (σA, σC and σm) on the carrying capacity (K), competition intensity (γ) and mutualistic benefit (b) in Eq.(1)

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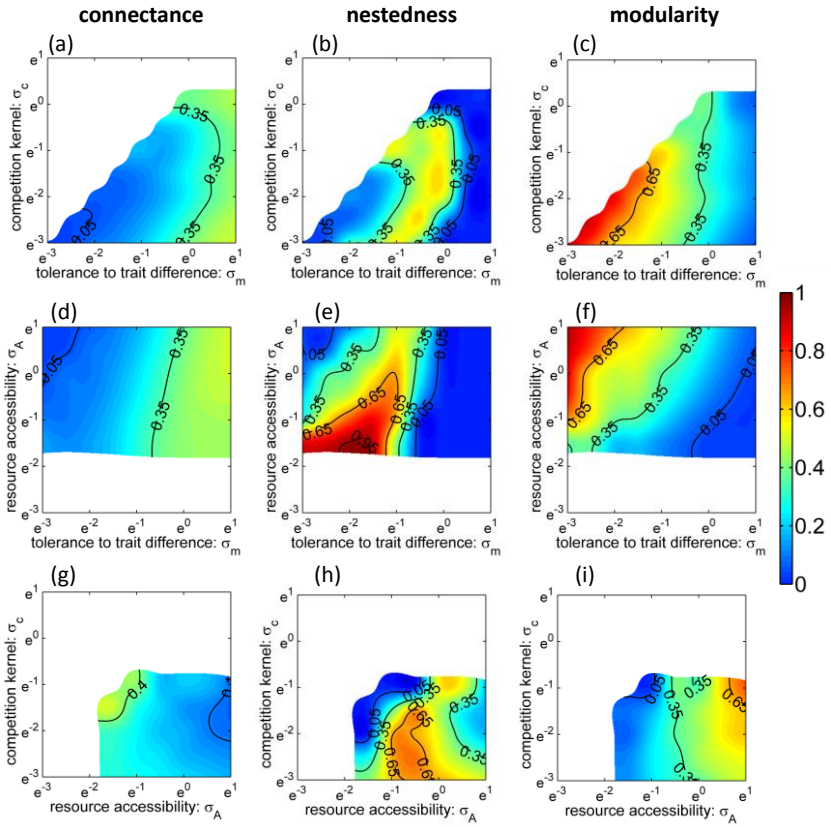
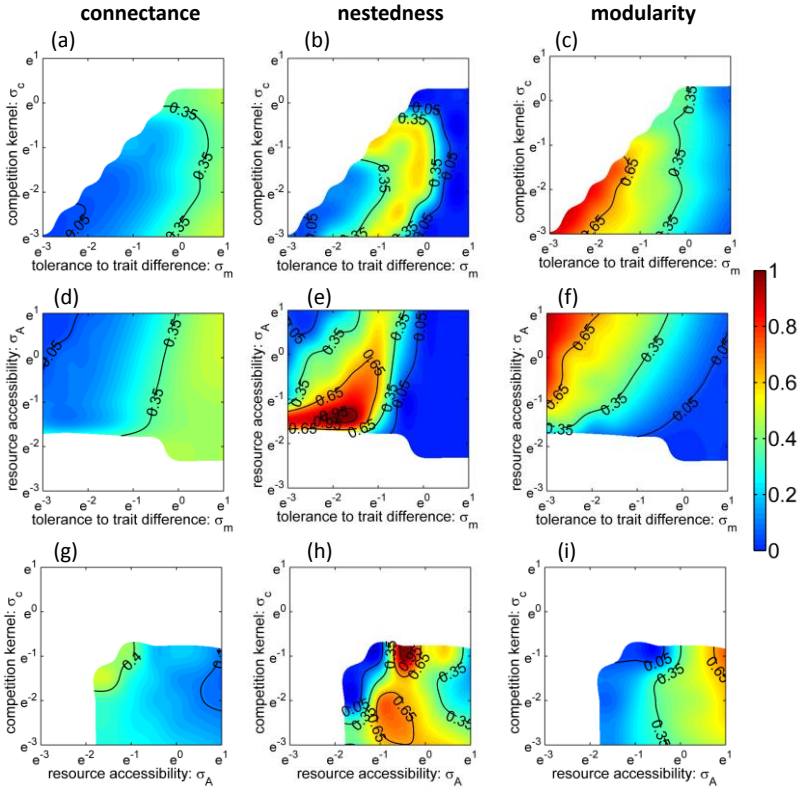
K_A=200



K_A=600



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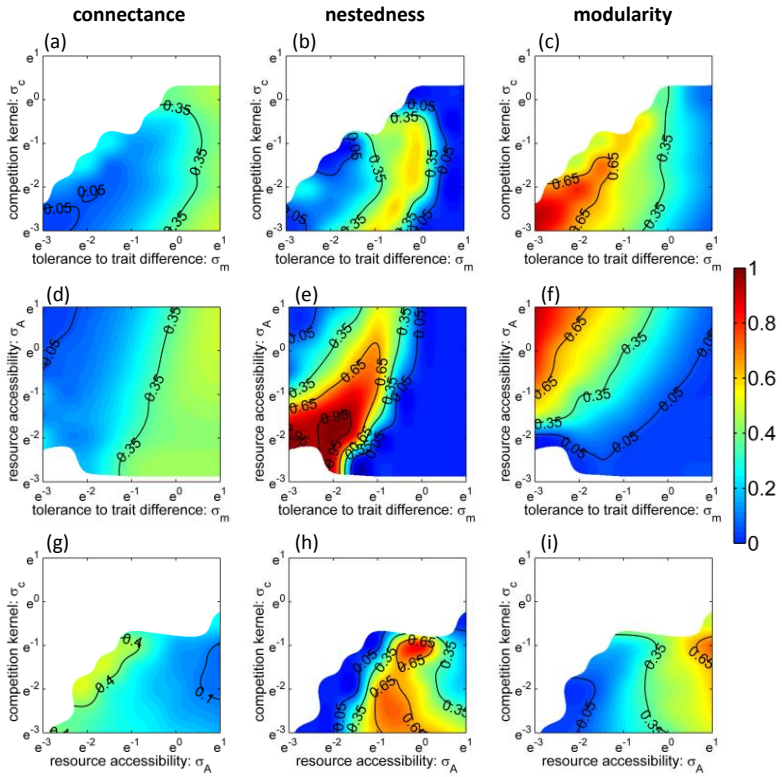
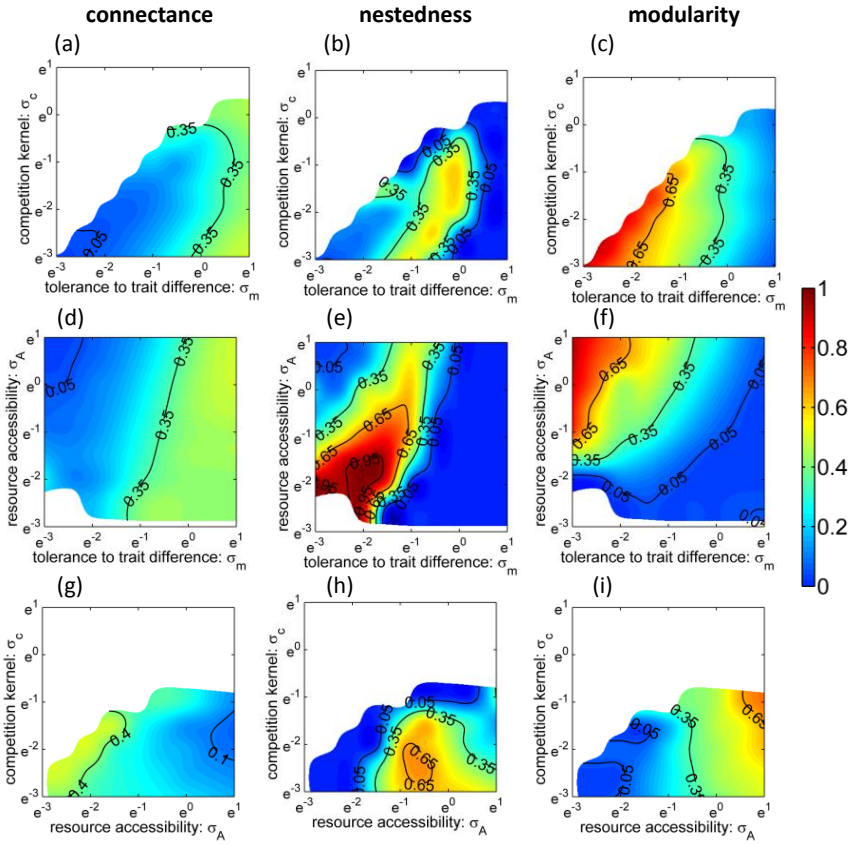
K_P=100



K_P=500



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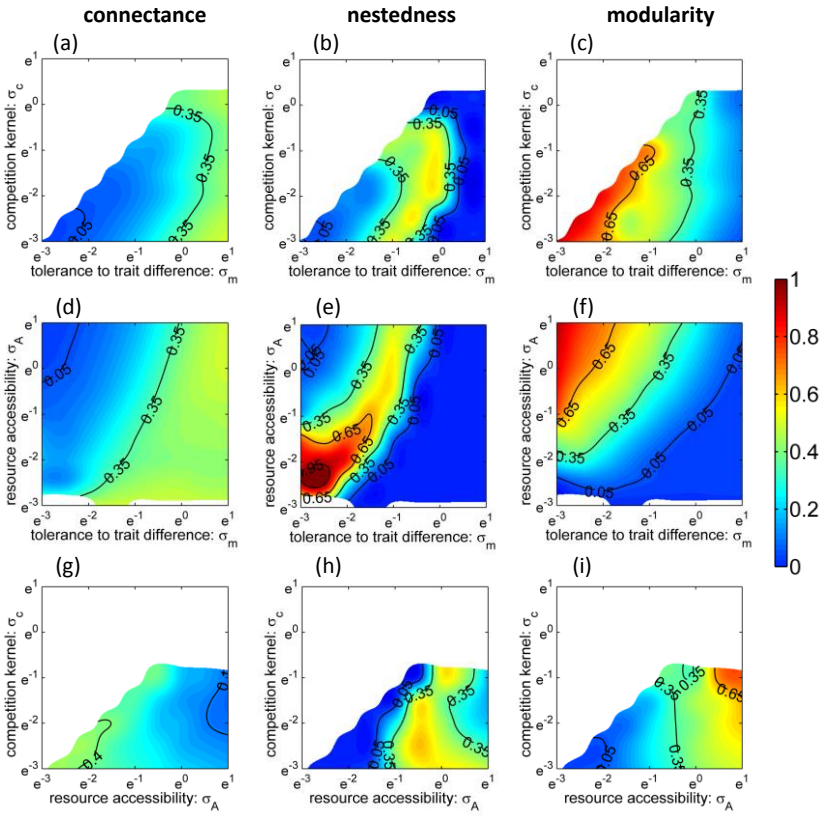
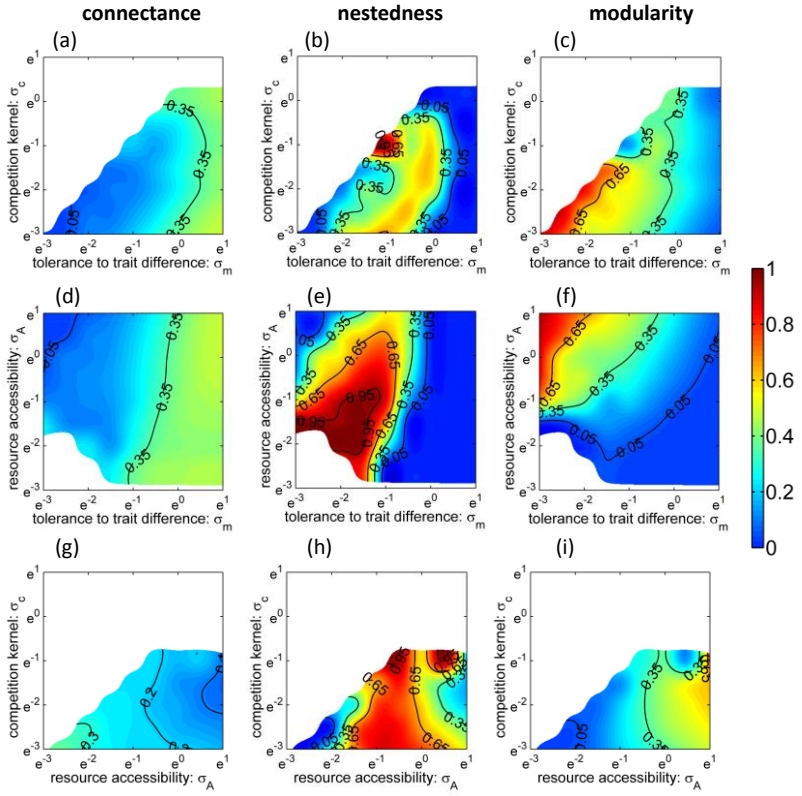
x_A^{max} =3; y_P^{max} =2.5



x_A^{max} =1; y_P^{max} =2.5



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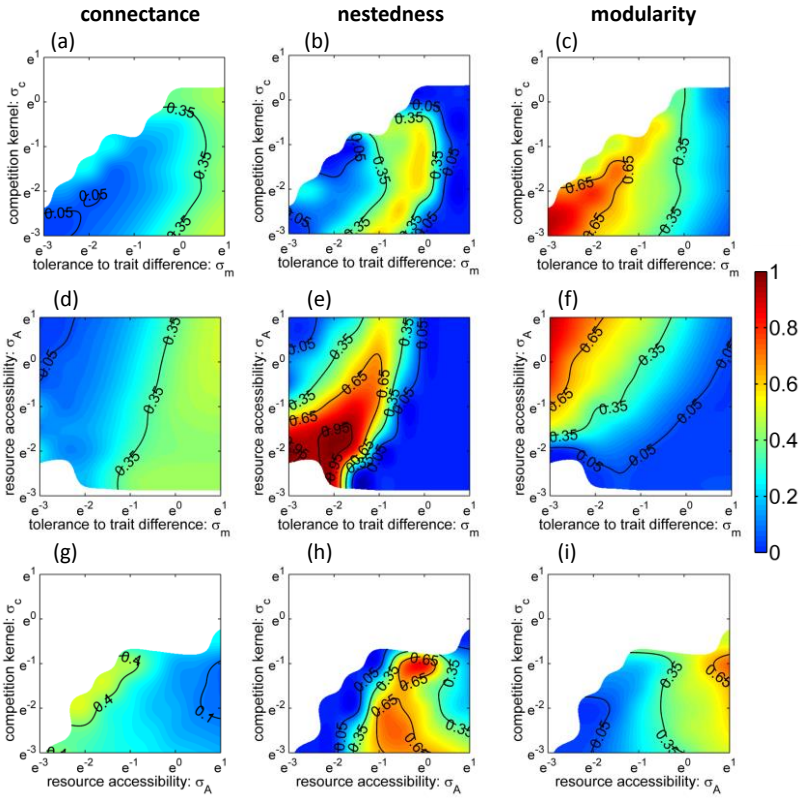
c=0.05



c=0.2

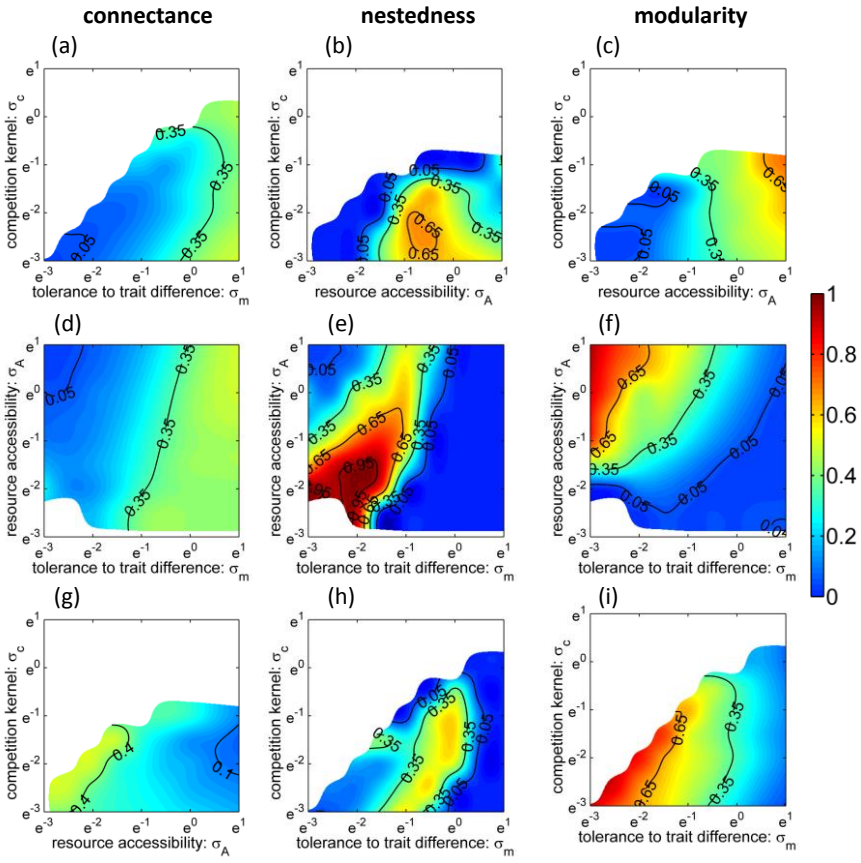


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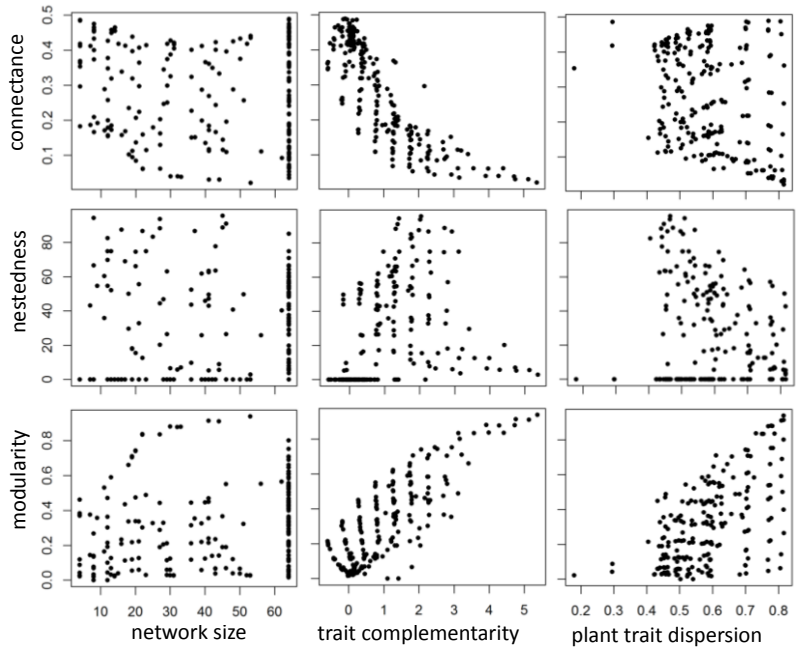
Figure S3: The quantitative connectance (first column), weighted nestedness (second column) and quantitative modularity (third column) of emerged networks as a function of model parameters (σ_A, σ_c and σ_m). Specifically, in each plot we varied two parameters and kept the third parameter fixed. The fixed parameters are $\sigma_A = e^{0.75}$ for the first row, $\sigma_c = e^{-3}$ for the second row, and $\sigma_m = e^{-1}$ for the third role, respectively. Remaining parameters are the same as stated in the main text, except the one specified at the top of each plot, for the purpose of testing parameter sensitivity.

K_A=200



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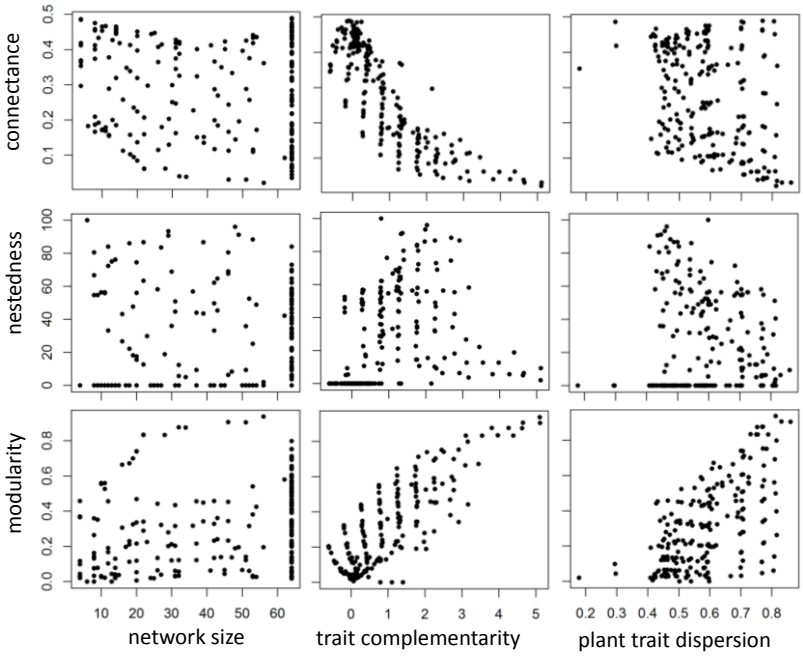

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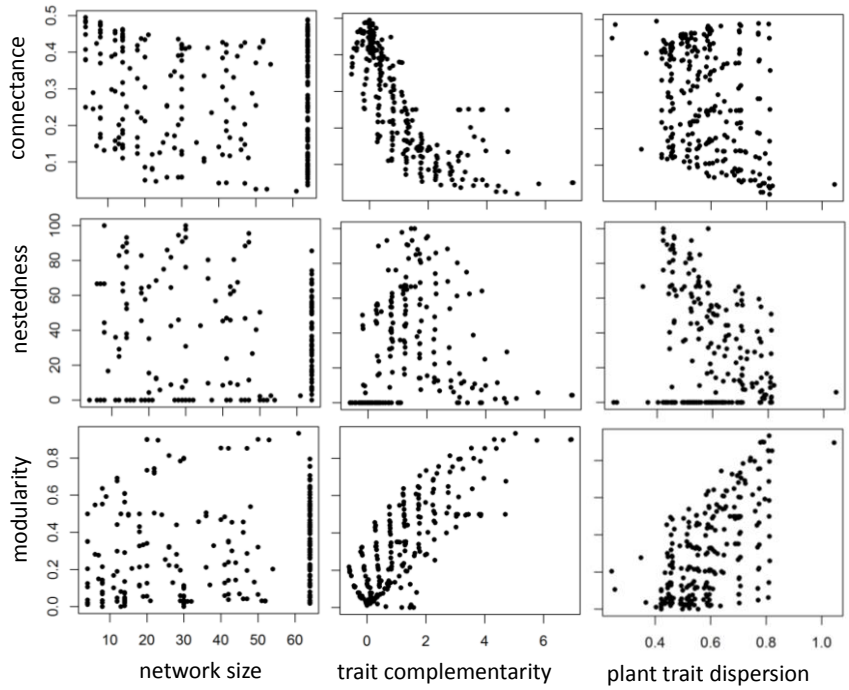
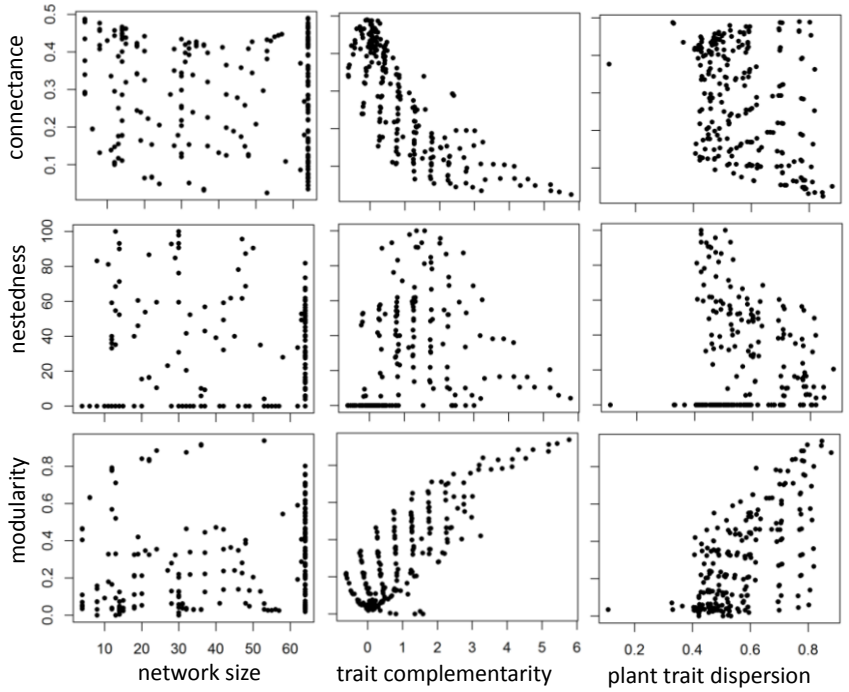
K_P=100



K_P=500



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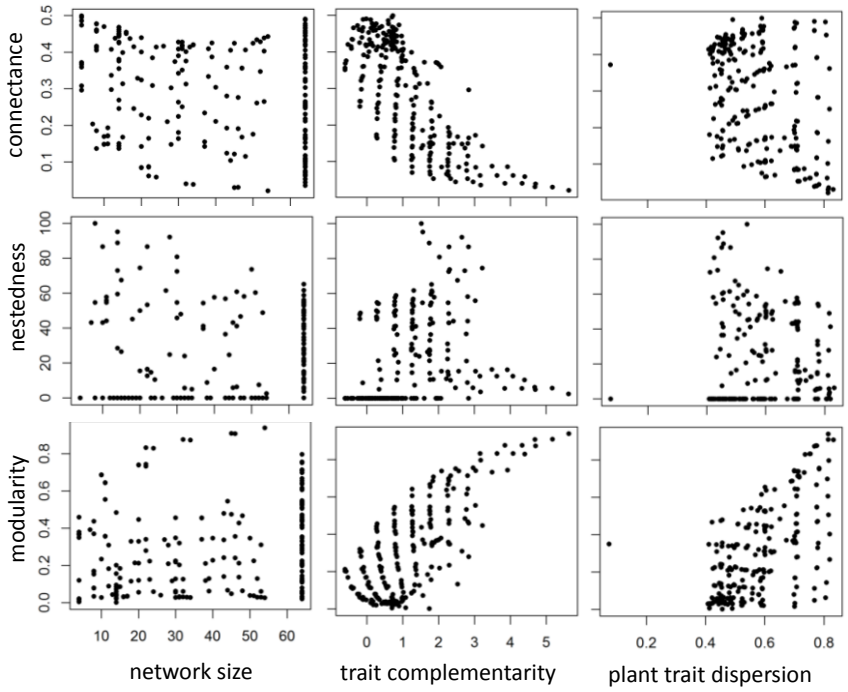
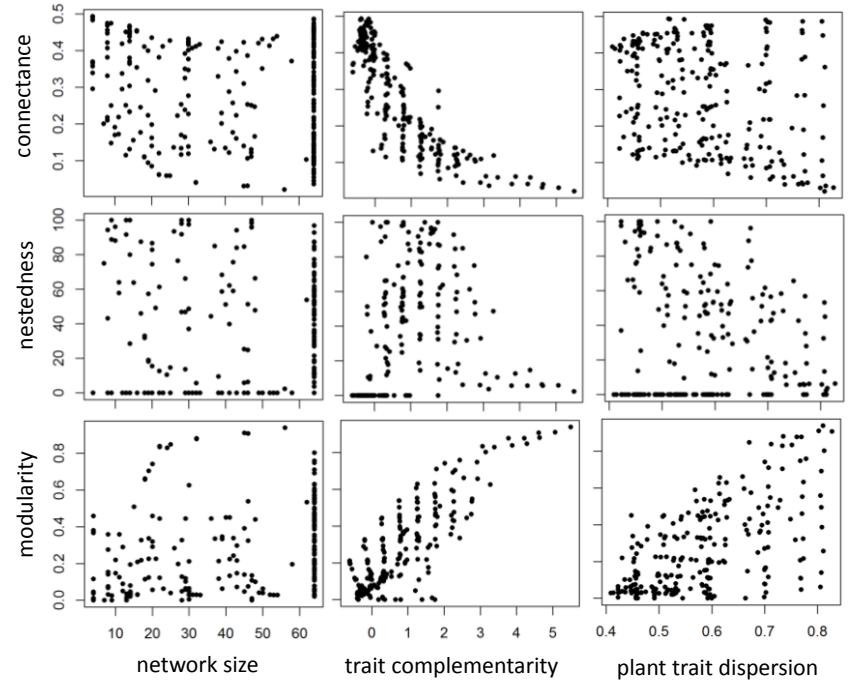
x_A^{max} =3; y_P^{max} =2.5



x_A^{max} =1; y_P^{max} =2.5



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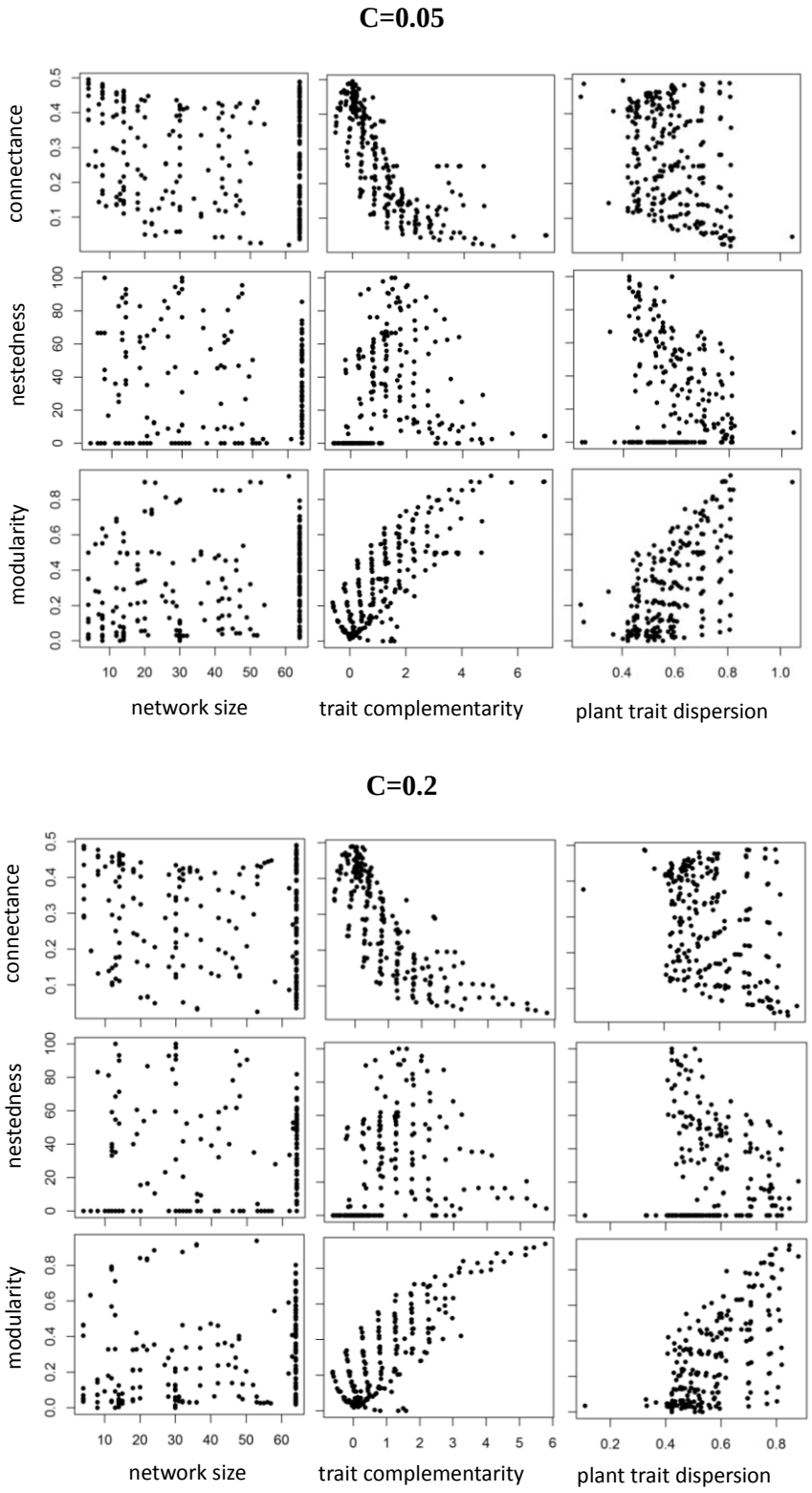

Figure S4: Relationships between network structures (connectance, nestedness and modularity) and explanatory variables (network size, trait complementarity, plant trait dispersion). Parameters are the same as stated in the main text, except those specified at the top of each plot, for the purpose of testing parameter sensitivity.

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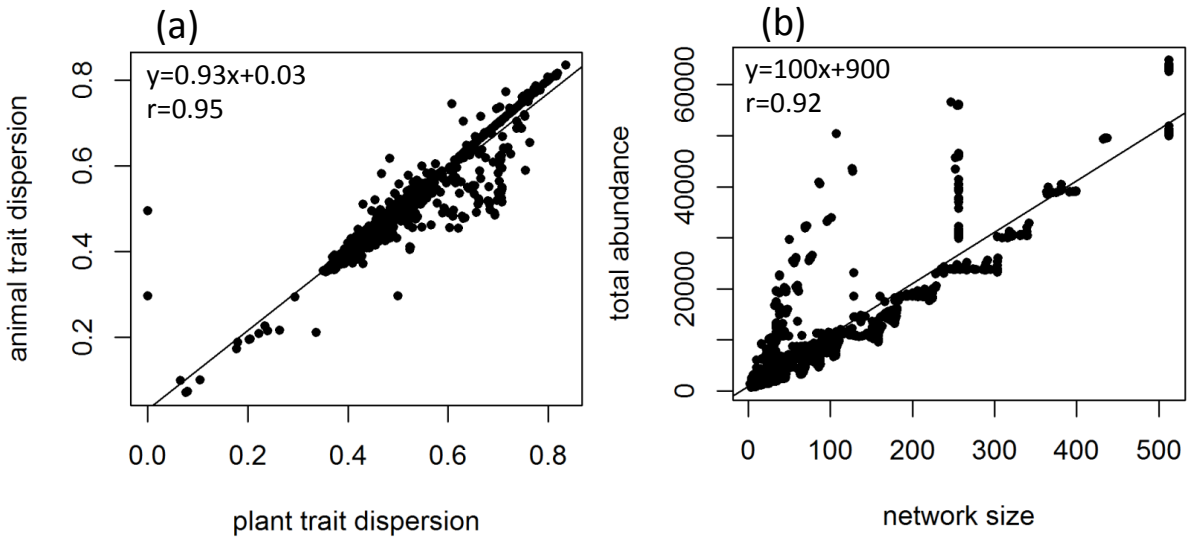

Figure S5: Strong positive correlation between predictor variables. (a) Animal trait dispersion with respect to plant trait dispersion. (b) Total population abundance with respect to network size. Lines are from the ordinary least square regression.

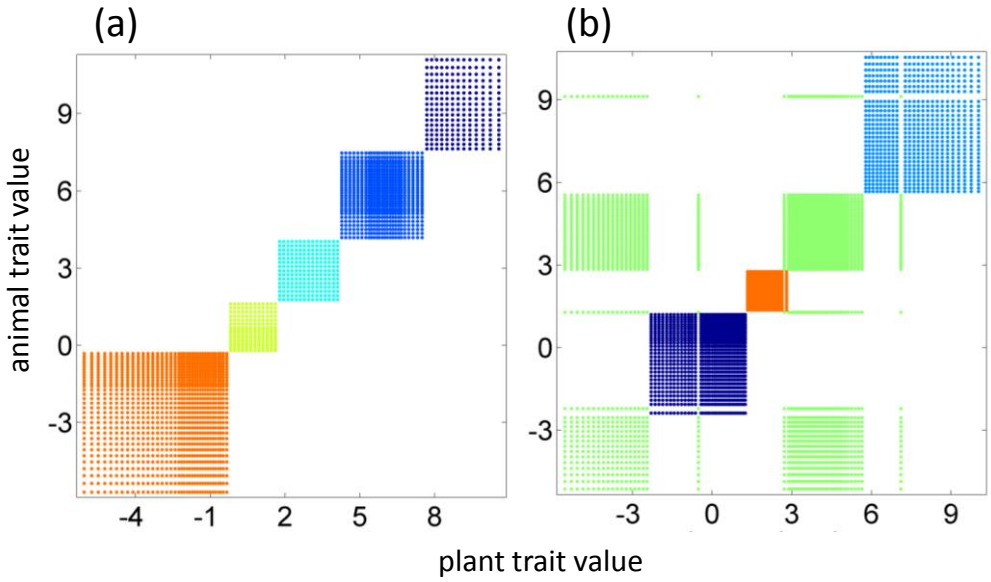

Figure S6: Modules observed in two simulated networks. Each pair of animal and plant traits belonging to the same module shares the same colour. (a) Evidence of strong association between trait complementarity and modularity; Parameters: $\sigma_A = e^{1}$, $\sigma_C = e^{-2}$, $\sigma_m = e^{-1}$. (b) Pairs having non-similar trait values are observed within the same module; Parameters: $\sigma_A = e^{1}$, $\sigma_C = e^{-2.25}$, $\sigma_m = e^{-1}$.

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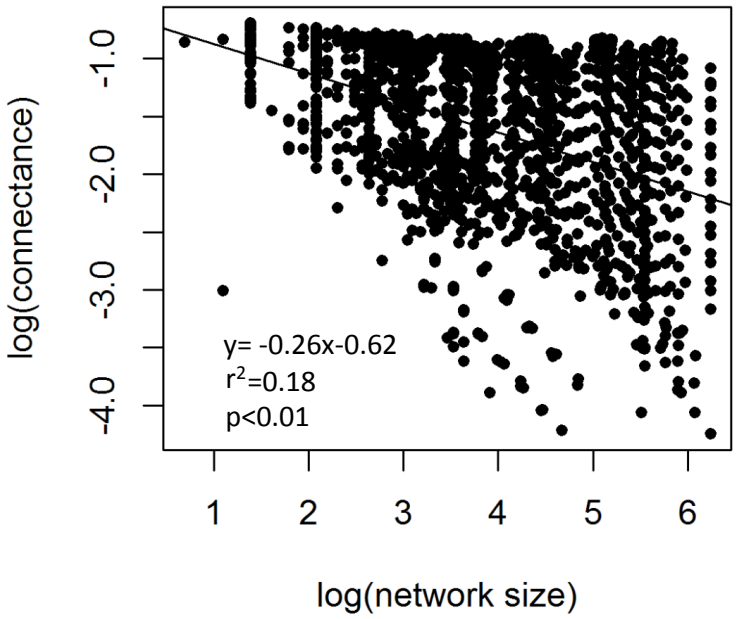

Figure S7: The log-log relationship between connectance and networks size

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CHAPTER 5

Invading a mutualistic network: To be or not to be similar

"In general, the pattern of invasion is that invaders become more intense the farther they enter alien territory, to the point where the native rulership cannot overcome them."

Sun Tzu, In *The Art of War*

Submitted to the Journal of Evolutionary Biology

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ABSTRACT

Biological invasion remains a major threat to biodiversity in general and a disruptor to mutualistic interactions in particular. While a number of empirical studies have directly explored the role of invasion in mutualistic pollination networks, a clear picture is yet to emerge and a theoretical model for comprehension still lacking. Here, using an eco-evolutionary model of bipartite mutualistic networks with trait-mediated interactions, we systematically explore invader trait, propagule pressure and network features of recipient community that contribute importantly to the success and impact of an invasion. High level of invasiveness is observed when invader trait differs from, and level of interaction generalization equals to, the community average, with declining propagules in multiple introductions. Surprisingly, the most successful invader is not always the one having the biggest impact. The network structure of recipient community, such as nestedness and modularity, is not a primary indicator of its invasibility; rather, the invasibility is best correlated with measurements of network stability such as robustness, resilience and disruptiveness (a measure of evolutionary instability). Our model encompasses more general scenarios than previously studied in predicting invasion success and impact in mutualistic networks, and our results highlight the need for coupling eco-evolutionary processes to resolve the invasion dilemma.

Keywords: mutualistic networks, invasiveness, invasibility, robustness, resilience, diruptiveness

1- Introduction

Rapid global changes induced by anthropogenic disturbance constitute a major threat to networks of ecological interactions (Tylianakis et al. 2008; Burkle & Alarcón 2011), of which biological invasion represents one important component (Morales & Traveset 2009; McGeoch et al. 2010). Mutualistic networks of pollination and seed dispersal are key service providers in ecosystems (Bronstein 2001); understanding how their structures and stabilities respond to biological invasions is paramount to safeguarding ecosystem function and service in a changing world (Traveset & Richardson 2006; Lurgi et al. 2014; Campbell et al. 2015). For efficient prevention and control, the challenge is to foresee the invasiveness and impact of potential invaders in given ecosystems. This is a challenge of complexity as no universal

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rules, except propagule pressure (Williamson 1996; Jeschke & Strayer 2006; Simberloff 2009), govern the process and success of invasion which are nearly exclusively contingent on the taxa and context (Williamson & Fitter 1996).

When introduced into a new environment, an alien species need to compete for space and resources with native resident species, simply by possessing certain phenotypic and behavioural traits (Romanuk et al. 2009). The strength of ecological interactions is often mediated by matching between functional traits of interacting species (Jousselin et al. 2003; Santamaría & Gironés 2007; Stang et al. 2009). A certain degree of similarity between the trait of invasive and resident species often indicates a strong mutualistic interaction (Gibson et al. 2012). Nevertheless, species with high invasiveness and impact in pollination networks acquire traits atypical of native (Aizen et al. 2008; Campbell et al. 2015; but see Morales & Traveset 2009). As such, features of both invaders and recipient communities play critical roles in predicting the success and impact, two interdependent elements, of an invasion (Shea & Chesson 2002; Gurevitch et al. 2011).

Such interdependence of invasiveness and impact could be further amplified in an ecological network because of cascading interactions (Dunne & Williams 2009; Bascompte & Stouffer 2009; Traveset & Richardson 2014). A high level of interaction generalization has been shown to determine the invasion success in both food webs (Romanuk et al. 2009; Lurgi et al. 2014) and mutualistic networks (Traveset & Richardson 2014). For instance, functional traits controlling feeding range such as having a large body size can promote invasion success (Lurgi et al. 2014). Invasive plants in pollination networks often have higher levels of interaction generalization than natives (Albrecht et al. 2014). The overall interactions in a pollination network can even be monopolized by super-generalist invaders (Aizen et al. 2008; Bartomeus et al. 2008; Vilà et al. 2009).

Characteristics of a recipient ecosystem responsible for its susceptibility to the establishment and spread of invasive species, defines its invasibility (Lonsdale 1999; Alpert et al. 2000). Besides physical factors such as habitat suitability and heterogeneity, other major characteristics considered in literature include the network architecture of biotic interactions. For example, a high level of network connectance – the proportion of realised interactions among possible ones – has been predicted to enhance the resistance of food webs to invasion (Romanuk et al. 2009), although contested by others to be otherwise (Baiser et al. 2010; Lurgi et al. 2014). Modularity – the extent to which a network is organized into groups of

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species interacting more strongly with species from the same group rather than from other groups – is observed to be lower in invaded pollination networks and food webs than in uninvaded ones (Albrecht et al. 2014; Lurgi et al. 2014). Empirical studies have also revealed that invaded pollination networks are more nested – where specialists interact only with a subset of species with which generalists interact – and normally contain a higher number of species than uninvaded networks (Padrón et al. 2009; Stouffer et al. 2014).

Mutualistic interactions normally have a facilitative effect on the establishment of alien species (Traveset & Richardson 2014). Successful invaders in mutualistic networks have been shown to interact with either the most specialist natives (Stouffer et al. 2014) or the most generalist ones (Padrón et al. 2009). However, empirical observations do not allow for discerning whether some network features could have triggered the invasion or are indeed resulting from the invasion. By comparing the pre- and post-invasion architectures of simulated pollination networks, Campbell et al. (2015) managed to fill the gap in literature and found that, while network connectance decreased, nestedness increased from invasions.

The role of particular network architectures in stabilizing networks has been hotly debated, especially regarding mutualistic networks. On one side, patterns of connectance and nestedness observed in mutualistic networks can facilitate the coexistence of species and thus contribute positively to network stability (Bastolla et al. 2009; Thébault & Fontaine 2010; Rohr et al. 2014). Network complexity, measured as network size and connectivity (number of interactions) can enhance network resilience (Okuyama & Holland 2008). On the other side, some theoretical studies have shown that these typical features specific to mutualistic networks can also be detrimental to network stability. For instance, extreme nestedness can destabilize the community (Campbell et al. 2012), modularity affects negatively on the stability of mutualistic networks (Thébault & Fontaine 2010). When interaction strength is further considered, stability becomes negatively associated with high levels of connectance and nestedness (Allesina & Tang 2012; Vieira & Almeida-Neto 2015).

Inconsistency of the correlation between network structure and network stability is somewhat caused by the confusion in choosing appropriate measures of network stability. Each metric of network stability only measures one specific facet of stability and thus often leads to contradictions when interpreted as the general stability for comparison (Vallina & Quéré 2011). Among these metrics of network stability/instability, network invasibility is a recent emergent concept particularly relevant to invasion biology; it is defined as the amount

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of opportunity niches in the trait space that allow for positive per-capita population growth of rare aliens (Hui et al. 2015). It is therefore necessary to explore how the concept of invasibility relates to these other measures of network stability/instability, as well as how these stability measures (including invasibility) are correlated with network architectures and the invasiveness of aliens.

Here, we deploy a theoretical approach to explore the process of biological invasion in mutualistic networks. Mutualistic networks are modelled using an eco-evolutionary model depicting simultaneously ecological dynamics of population densities happening at a faster time scale and evolutionary dynamics of functional traits happening at a slower time scale, using the framework of adaptive dynamics (Metz et al. 1992; Dieckmann & Law 1996). In these networks, each species is identified by its trait (i.e. as morphospecies) which determines the intensity of both intra-specific competition and mutualistic interaction. Our previous work has shown that properties of the mutualistic networks emerging from this model are comparable with features of empirical networks (Minoarivelo & Hui 2015). Here, we first use the model to generate mutualistic networks as recipient communities, into which we then introduce an alien species. By examining a wide range of possibilities for both invaders and recipient communities, we investigate how they respond to each other. In particular, we study (i) how the invasiveness and the impact of an introduced species depend on whether or not its trait and its level of interaction generalization are relatively similar to the average of the recipient community; (ii) how the success of an invasion depends on the way the invasive species is introduced, i.e. propagule pressure; (iii) how the invasibility and other metrics of network stability depend, or not, on the structure of recipient communities.

2- Materials and methods

Evolutionary and ecological processes are coupled. Evolutionary changes in functional traits can affect ecological processes such as the way species interact with each other and subsequently the behaviour of population dynamics and demography. In return, functional traits evolve in response to varying frequency-dependent selection from changing population densities. As such, we design a model of mutualistic network emergence, implementing exactly such coupling of population dynamics and trait evolution. Specifically, we assume that resource competition becomes intense when the two species involved have similar traits, as illustrated in the limiting similarity theory (Abrams 1983), and that matching traits between a pair of mutualistically interacting animal and plant species (i.e. assortative

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interactions) can expect high fitness rewards. For pollination syndromes, pollinator trait could be its proboscis length, and floral trait could be the length of pollen tube. For seed dispersal syndromes, traits could be the body size of animal dispersers, or the fruit size of the plant. Following the framework of adaptive dynamics, traits can evolve either directionally or disruptively, and the latter case allows a single trait to diversify adaptively into two, eventually forming an ecological network. The resultant network will be considered as a native mutualistic community into which we introduce an alien species. Here we focus on examining the traits of successful invaders and the network features of recipient communities which resist the invasion.

Ecological dynamics

Let there be n morphospecies of animals and m morphospecies of plants. Each morphospecies, indexed by i for animals and j for plants, is further characterized by its population density A_i (for $i \in 1,...,n$) and P_j (for $j \in 1,...,m$), respectively. We denote the trait of animal morph i by x_i and the trait of plant morph j by y_j. The population dynamics of the system is governed by the per-capita population growth rates, dependent on the intrinsic growth rate, intra-trophic competition and cross-trophic mutualistic interactions (following Holling's type II functional response (1959)) (Holland et al. 2006; Zhang et al. 2011; Nuwagaba et al. 2015; Minoarivelo & Hui 2015):

$$\frac{dA_i}{A_i dt} = f_A(x_i) = r_A - \frac{r_A \sum_k \gamma(x_i, x_k) A_k}{K_A(x_i)} + \frac{\sum_j b_{A_i P_j} w_{A_i P_j} P_j}{1 + h \sum_j w_{A_i P_j} P_j}, \quad (1a)$$

$$\frac{dP_j}{P_j dt} = f_P(y_j) = r_P - \frac{r_P \sum_k \gamma(y_j, y_k) P_k}{K_P(y_j)} + \frac{\sum_i b_{P_j A_i} w_{P_j A_i} A_i}{1 + h \sum_i w_{P_j A_i} A_i}, \quad (1b)$$

where r is the intrinsic population growth rate, and h the handling time that animals spend for visiting a plant and digesting the nutrients extracted from the plant; both are assumed to be trait-independent to avoid over-parameterization of the model (r_A = r_P =1; h = 0.1). Note that parameter values provided below in brackets are used as reference for sensitivity tests. In the following, all terms in Eq.(1b) can be mirrored from the specified formulation in Eq.(1a).

The carrying capacity, K_A and K_P, varies between morphs, representing trait-mediated resource accessibility. Following Doebeli & Dieckmann (2000), we used a Gaussian function

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for the carrying capacity: $K_A(x_i) = k_A N(x_A^{max}, \sigma_A, x_i)$, where k_A (= 400) is a scaling constant, and $N(x_A^{max}, \sigma_A, x_i)$ the Gaussian density function of trait x_i with the maximum carrying capacity at x_A^{max} (= 3) and the standard deviation σ_A. This means that there exists an optimal trait value for accessing resources at a maximum level k_A. Species with trait deviating from the optimal trait suffer from lower resource accessibility and thus lower carrying capacity. Similarly, we set the baseline values of k_P (= 300) and y_P^{max} (= 2) for the plant species in the following analysis.

The intra-trophic competition function γ is set to let morphs with more similar traits suffer stronger competition. We used a Gaussian function for depicting the competition intensity between morphs (Bürger et al. 2006; Doebeli & Dieckamann 2000; Raimundo et al. 2014): $\gamma(x_i, x_k) = \exp(-(x_i - x_k)^2 / 2\sigma_C^2)$, where σ_C controls the width of the competition kernel. This means that intra-trophic competition becomes less sensitive to trait difference between the two competing species as the width of competition kernel σ_C becomes larger. In such a case, species can compete with a wider range of other species for resources.

The cross-trophic mutualistic benefit, b_{AP}, reflects the assumption of assortative interactions that matched traits bring to each other high profit, and is also assumed to follow a Gaussian function of trait difference: $b_{AP}(x_i, y_j) = c \cdot \exp(-(x_i - y_j)^2 / 2\sigma_m^2)$, where c (= 0.1) is a parameter controlling the magnitude of the maximum mutualistic support, and the parameter σ_m controls the tolerance level of successful interactions to the dissimilarity of involved traits (Nuismer et al. 2010). This means that a species having trait value similar to its mutualistic partner gains the highest mutualistic benefit. As the tolerance level to trait difference (σ_m) becomes smaller, mutualistic benefits can only be assured for partners having very similar traits. A high level of tolerance to trait difference means that partner species with dissimilar traits can also gain rewards from their mutualistic interactions.

The interaction preference of two morphs w_{AP} determines the possibility of interaction after the encounter and is assumed to follow adaptive foraging strategies, depending on both the benefit and abundance of involved morphs (Doebeli & Dieckmann 2000; Zhang & Hui 2014). Modifying the expression which describes the strength of mutualistic support in Doebeli & Dieckmann (2000), we have the following function for the adaptive interaction preference: $w_{A_iP_j} = b_{A_iP_j} \Sigma_k A_k / \Sigma_k A_k b_{A_kP_j}$, where the summation term $\Sigma_k A_k$ in the numerator is

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for normalization. This means that an animal prefers to interact with plants that are common and with matching traits.

Evolutionary dynamics

Functional traits of interacting morphs are subject to mutations. This can also be interpreted as the replacement and reassembling of local species through colonization of regional species with different traits to these local residents. Mutation normally happens at a low rate so that the populations can be considered at their ecological equilibriums when the mutation occurs (Doebeli & Dieckmann 2000). We only consider the non-trivial strictly positive and asymptotically stable equilibrium points of the system ($\tilde{A}_i(x_i, y_j)$ and $\tilde{P}_j(x_i, y_j)$). When a mutation enters the system, the resident morphospecies and the mutant undergo an intra-trophic competition determined by Eq.(1). Let x_i' and y_j' be the mutant trait of animal morphospecies *i* and plant morphospecies *j*, and let $X = (x_1,...,x_n)$ and $Y = (y_1,...,y_m)$ be the trait vectors of the resident morphospecies. We can define the invasion fitness of the rare mutants at the equilibrium points as their per-capita growth rates when setting their initial densities to be negligible: $f_A(x_i')$ and $f_P(y_j')$. The selection gradient, defined as $g_{A_i} = \partial f_A(x_i')/\partial x_i'|_{x_i'=x_i}$ and $g_{P_j} = \partial f_P(y_j')/\partial y_j'|_{y_j'=y_j}$, determine the direction and speed of trait evolution, and an evolutionary singularity is defined as the traits $(\tilde{x}_i, \tilde{y}_j)$ when the selection gradient disappears.

The evolutionary dynamics of the functional traits can be depicted by the canonical equations of adaptive dynamics (Dieckmann & Law 1996):

$$\begin{aligned} dx_i/dt &= m_A \tilde{A}_i g_{A_i} \\ dy_j/dt &= m_P \tilde{P}_j g_{P_j} \end{aligned}, \qquad (2)$$

where m_A and m_P are parameters proportional to the rate and variation of the mutation (set to 10^{-3}) in the analysis. An evolutionary branching is to occur in the system provided that three conditions are satisfied. First, the singularity $(\tilde{x}_i, \tilde{y}_j)$ should be an evolutionary attractor of directional selection; that is, it is convergence stable. This happens when all eigenvalues of the Jacobian matrix of Eq.(2) have negative real parts (see Doebeli & Dieckmann 2000); this means $\partial g_{A_i}/\partial x_i|_{x_i=\tilde{x}_i} < 0$ and $\partial g_{P_j}/\partial y_j|_{y_j=\tilde{y}_j} < 0$. Second, the singularity should represent a

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fitness minimum to induce disruptive selection and to allow the mutant to invade (Geritz et al. 1998); that is, $\partial^2 f_A / \partial x_i'^2 |_{x_i'=\tilde{x}_i} > 0$ and $\partial^2 f_P / \partial y_j'^2 |_{y_j'=\tilde{y}_j} > 0$. Finally, the mutant and the resident morphospecies need to coexist to ensure the protection of dimorphism from the evolutionary branching (Geritz et al. 1998); that is, the two morphospecies can invade each other: $(\partial^2 f_A / \partial x_i^{\,2} + \partial^2 f_A / \partial x_i'^2) |_{x_i'=x_i=\tilde{x}} > 0$ and $(\partial^2 f_P / \partial y_j^2 + \partial^2 f_P / \partial y_j'^2) |_{y_j'=y_j=\tilde{y}_j} > 0$.

Numerical simulation

We numerically solved the population dynamics (Eq.(1)) and the canonical equations of adaptive dynamics (Eq.(2)). It is worth noting that, although the trait of a species can take any values (e.g. log-transformed body size as a focal trait can range from negative to positive infinity, theoretically speaking), only those that are feasible and can ensure its own viability, i.e. with a positive equilibrium in Eq.(1), can be realised in the model. Once the system reaches its singularity, the three conditions for evolutionary branching will be examined. If satisfied, a new morphospecies will be added to the system with its trait value slightly different from the resident trait (+0.01) and having a low initial density (10% of its resident population density). The density of the resident morphospecies will be simultaneously updated to be 90% of its original. The process was repeated until we obtain sufficient number of morphospecies in the community and the system has reached its singularity (no directional selection). A morphospecies was considered extinct when its population density dropped below 10^{-8}.

We distinguished three types of communities depending on their sizes. Small communities were generated by allowing the system to branch four consecutive times, giving a maximum number of 16 ($=2^4$) morphs on each side of animals and plants. An example of the formation of a small community by trait evolution depicted as evolutionary trees is given in Fig.1. Medium-size communities were generated by five consecutive branching events, giving a maximum of 32 ($=2^5$) morphs on each side. Large communities were obtained by six consecutive branching events with a maximum of 64 ($=2^6$) morphs on each side. We obtained communities with different structures by varying kernel parameters (Minoarivelo & Hui 2015): the width of the intra-trophic competition kernel (σ_C), the tolerance to trait difference in a mutualistic interaction (σ_m) and the width of resources accessibility (σ_A for animals and σ_P for plants; we keep $\sigma_A = \sigma_P$ for simplicity). These parameters were varied from e^{-3} (≈ 0.05) to

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e, with a multiplicative step of $e^{1/4}$. We discarded the combinations of σ_C, σ_m and σ_A that resulted in monomorphic systems (no diversification).

Network analysis

We considered the bipartite mutualistic networks formed by interactions between the two sets of animal and plant morphospecies. Here, we depicted the network as a quantitative interaction matrix (Q) where its elements (q_{ij}) represent the interaction strength between animal *i* and plant *j*. Following Berlow et al. (2004), we define the interaction strength as the non-linear functional response term of Eq.(1), depending on both the number of recruited animal *i* from interacting with plant *j*, and the number of recruited plant *j* from interacting with animal *i*, per time unit:

$$q_{ij} = \frac{1}{2}\left(\frac{A_i b_{A_i P_j} w_{A_i P_j} P_j}{1 + h w_{A_i P_j} P_j} + \frac{P_j b_{P_j A_i} w_{P_j A_i} A_i}{1 + h w_{P_j A_i} A_i} \right). \qquad (3)$$

When the element q_{ij} is less than 10^{-8}, it was considered to be equal to zero, indicating a negligible interaction. An illustration of such interaction network as a bipartite weighted graph is given in Fig.1.

We analysed the architecture of the networks by using four metrics adapted for quantitative matrices. First, the level of specialization (*SPE*) of each network was measured according to the quantitative index H_2' of Blüthgen et al. (2006). This index measures the overall deviation of species' realized degrees from their expected ones, ranging from 0 (no specialization) to 1 (perfect specialization). Second, the quantitative connectance metric (*CON*) was computed as the quantitative linkage density divided by the number of species in the network (Tylianakis et al. 2007). Third, we used the metric WNODF (Weighted Nestedness metric based on Overlap and Decreasing Fill) for depicting the level of nestedness (*NEST*) (Almeida-Neto & Ulrich 2011). Finally, the level of modularity was measured using the algorithm *QuanBimo* (Dormann & Strauβ 2014). All these network metric measurements are implemented in the R library *bipartite* (Dormann et al. 2008).

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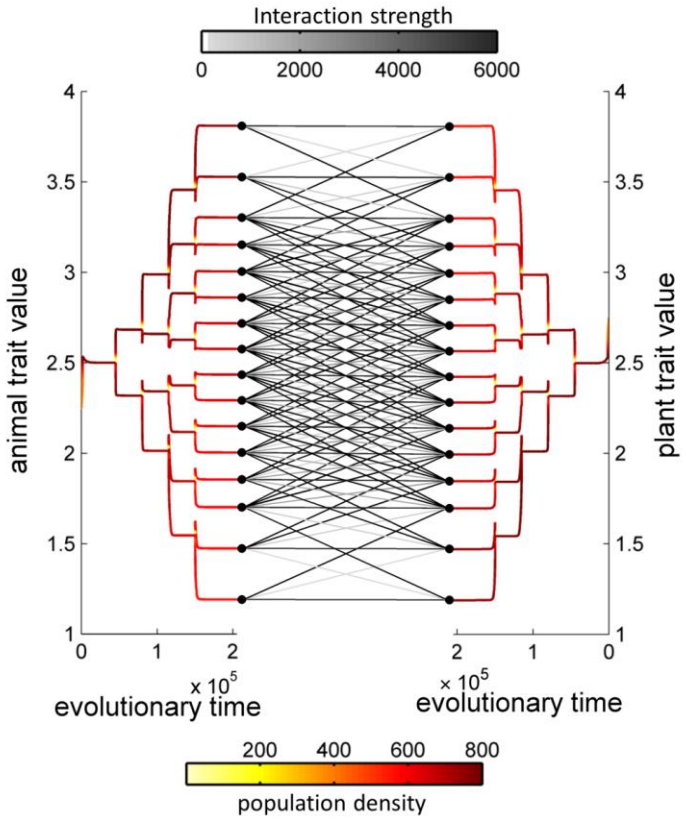

Figure 1: Evolutionary dynamics of a mutualistic network. The trait dynamics pre-invasion is represented as two evolutionary trees and its associated interaction network represented as a bipartite graph. Parameters: $\sigma_A = e^{0.75}$; (b) $\sigma_c = e^{-3}$; (c) $\sigma_m = e^{-2.25}$.

Invasion trial

As the model is symmetric regarding animals and plants side, we introduced an alien animal species into the native community, with the number of individuals introduced equal to 5%, 10% and 25% of the average population density in the recipient community. Because effects of biological invasion are generally studied at ecological time scales, we fixed the phenotypic traits of the studied community once the alien species was introduced and only allowed population densities to change according to Eq.(1).

To test the dependence of invasion success on the particular ways that these propagules were introduced, we randomly selected 100 medium sized networks and tested five different ways of introducing the alien propagules. First, all individuals of the alien species were introduced only once before letting population dynamics to change. Second,

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individuals of the alien species were divided into two groups of equal size. The first group was introduced at the initial time step while the second group after 5 time steps. Third, individuals of the alien species were introduced at three consecutive times separated by an interval of 5 time steps. The number of individuals introduced increased each time, representing 20%, 30% and 50% of the total propagule size. Fourth, individuals were introduced three times but with declining numbers each time (50%, 30% and 20%). Finally, we introduced the alien species five consecutive times with equal densities (20% each time), with introductions separated by 5 time steps.

We further investigated the role of the trait and the level of mutualism generalization of the invader, relative to the resident species in recipient communities. First, we introduced animal species with nine different trait values, ranging evenly from the lowest to the highest trait value of the natives. Hereafter, the trait value of the invader is reported as the relative trait value (*rtv*) and scaled between 0 (lowest trait value) to 1 (highest trait value), relative to the traits of resident species. Second, the level of mutualism generalization was measured as the tolerance of the invader to trait difference (i.e. σ_m) for feasible mutualistic interactions. A high tolerance to trait difference (large σ_m) suggests that mutualistic benefits can be assured by interacting with mutualistic partners with a wide range of traits, making the focal species a generalist. Nine levels of generalization of the invader were considered relative to the generalization level of the native community, with the generalization level ratio (*glr*) ranging from one fifth to five times the tolerance of native species to trait difference (σ_m).

We considered two measurements of invasion success: invasiveness of the alien species, and the impact it has on the native community. Invasiveness (*INVn*) was defined as the relative growth rate of the invader: $INVn = \ln(A_{final}^{inv} / A_{initial}^{inv})$ in which A_{final}^{inv} is the population density of the invader measured after the last possible introduction (i.e. at the 25th time step after the fifth introduction which was at the 20th time step), and $A_{initial}^{inv}$ the total number of propagules introduced. The impact of the invasion (*IMP*) was measured as the magnitude of change in the relative growth rate of the native species: $IMP = |\ln(A_{final}^{nat} / A_{initial}^{nat})|$ in which A_{final}^{nat} and $A_{initial}^{nat}$ denote the total population size of all native animals at the 25th time step and before the invasion, respectively.

Network stability and invasibility

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To assess the potential ability of native communities to resist to biological invasion, we used a set of 1000 networks, including 350 small, 370 medium-size and 280 large networks. We calculated all commonly used stability metrics for these 1000 networks. First, network resilience (*RES*) was measured as the logarithm of the absolute value of the dominant eigenvalue of the Jacobian matrix at equilibrium (DeAngelis 1980; Okuyama & Holland 2008; Encinas-Viso et al. 2012): $RES = \ln|\lambda|$. Specifically, the Jacobian matrix of the population dynamics (Eq.(1)) was computed at system singularity before alien introduction. Network resilience depicts how quickly a system returns to its steady state after being perturbed (DeAngelis 1980). Second, we calculated network robustness (*ROB*) based on the concept of network response (secondary extinctions) from species removal (Dunne et al., 2002). Robustness is the fraction of species that had to be removed, from generalist to specialist, to result in the loss of more than 50% of all species. Finally, disruptiveness (*DIS*), a measure of evolutionary instability, was computed as the average of the strength of disruptive selection for all animal species (Brännström et al. 2011), with the strength of disruptive selection for a particular species *i* measured as the curvature of its invasion fitness at the singularity trait value $\tilde{x}_i$: $\sum_{i=1}^{n} \partial^2 f_A / \partial x_i'^2 |_{x_i'=\tilde{x}_i}$.

We calculated the network invasibility (*INVb*) as the probability (proportion) of successful invasions (i.e. with positive invasiveness) among all invaders with traits spanning across the entire native trait range. We calculated the invasiveness and impact of an alien species when invading these 1000 networks. We assign each invader a trait as the average of native traits weighted by their population densities and a level of mutualistic generalization similar to the native community (*glr*=1). We further assessed the relationship between network architecture (section 2.4) and stability metrics, including invasibility, using Spearman's rank correlation. We conducted a multidimensional scaling analysis of k-mean clustering and hierarchical clustering (*pvclust* library in R, Suzuki & Shimodaira 2015) based on the rank correlation matrix to group closely related network metrics and observables.

3- Results

Role of invasive trait

Both the generalization level of the invader and its trait had an effect on the invasion success (Fig.2). In general, species having the level of generalization similar to that of the natives are more likely to be invasive (vertically centred area of Fig.2a). Species having extreme trait

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values but a high level of generalization also have high invasiveness (top-right and bottom-right corners of Fig.2a). Species that are extreme specialist with extreme trait values also tend to be more invasive than those with trait value similar to most of the native species (extreme left area of Fig.2a). Although the trait of the invader and its level of generalization can affect the population density of the native community, the overall impact of the invasion is small, reducing the total population size of the entire native community by about 1% (Fig.2b). Highly generalist species having trait values similar to those of native species have the highest impact on the native community (centre-right area of Fig.2b). The impact is also high for extreme specialist species having trait values similar to natives (centre-left area of Fig.2b). The introduction of species having extreme trait values or having level of generalization similar to those of the natives only slightly affected native population densities (top, bottom and vertically centred areas of Fig.2b). For 89% of the studied cases, the introduction of the alien species made the total population density decline (Fig.S1).

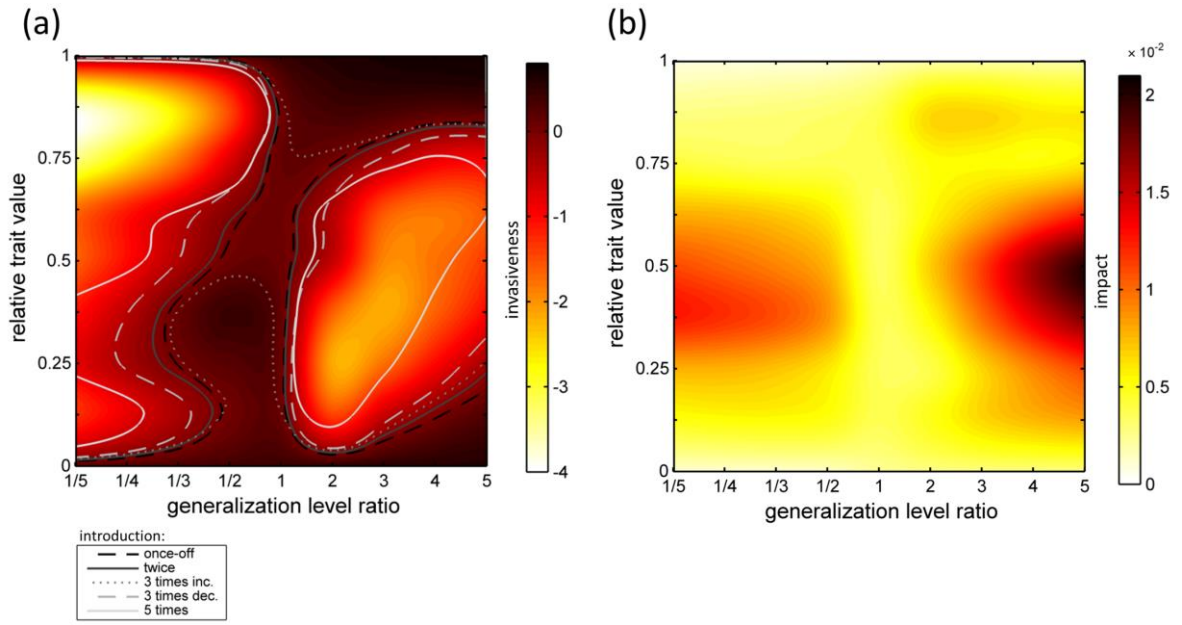

Figure 2: (a) Invasiveness and (b) impact of the invader as a function of its relative trait value and generalization level ratio, relative to those of the native community. Invasiveness and impact values represent the average over 100 medium-size networks. Lines represent the zero level of invasiveness under different introduction modes.

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Role of introduction mode

Invasion success also depends on the way these alien individuals are introduced (e.g. once-off or multiple introductions); that is, the introduction mode. However, the dependence of invasiveness on introduction mode is sensitive to the level of generalization of the invader. First, when an invader has the same level of generalization as the native species, its invasiveness becomes the highest for the mode of three introductions with decreasing propagule sizes, and becomes the lowest for the model of three introductions with increasing propagule sizes (Fig.3a, b). Second, when the invader is either more specialist or more generalist than the native species, the invasiveness of the alien becomes highly dependent on the number of introduction events, with higher numbers of introductions leading to high invasiveness (Fig.3c, d and FigS2).

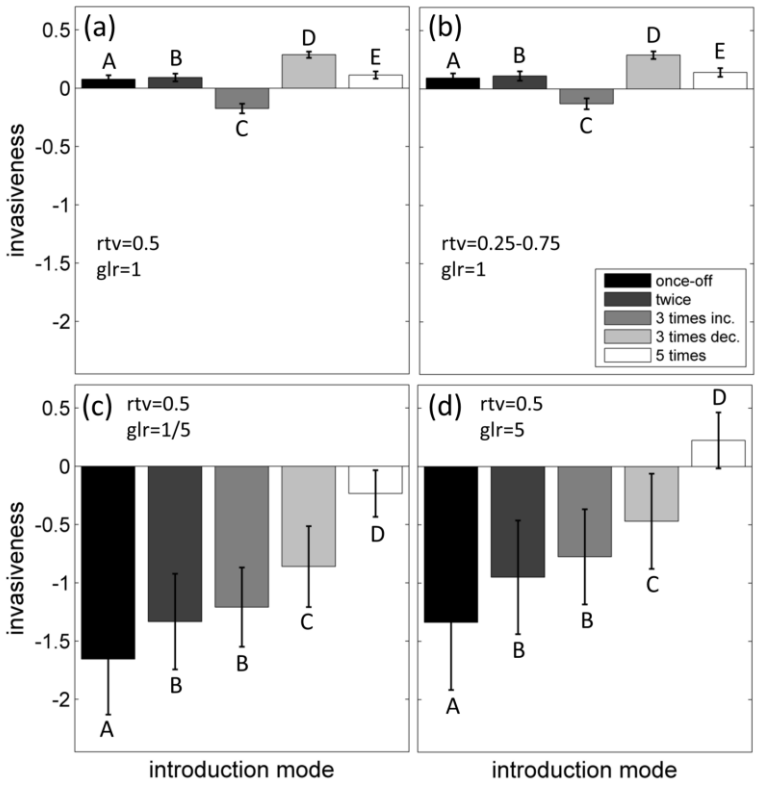

Figure 3: Average (over 100 medium-size networks) of the invasiveness when the alien has: (a) typical trait and similar level of generalization to the native species, (b) average trait and similar level of generalization to native species, (c) typical trait and is more specialist than native species, (d) typical trait and is more generalist than native. Error bars represent tenth of the standard deviation. *rtv*

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stands for relative trait value and *glr* for generalization level ratio. Bars with different characters are significantly different from each other.

The dependence of the invasion impact on the mode of introduction is uniform regardless of the invader trait value and its generalization level. The impact of the invasion on the population of the native community is highest when the invader is introduced three times with decreasing propagule sizes (Fig.4). However, when the invader species is highly specialist or highly generalist, the impact of multiple introductions is not significantly different from the impacts caused by a once-off introduction (Fig.4c, d). Regardless of the introduction mode (Fig.S2, Fig.S3) and the initial propagule size (Fig.S4), these patterns demonstrated in the previous section regarding the dependence of invasiveness and impact on the invader trait and its level of generalization remained.

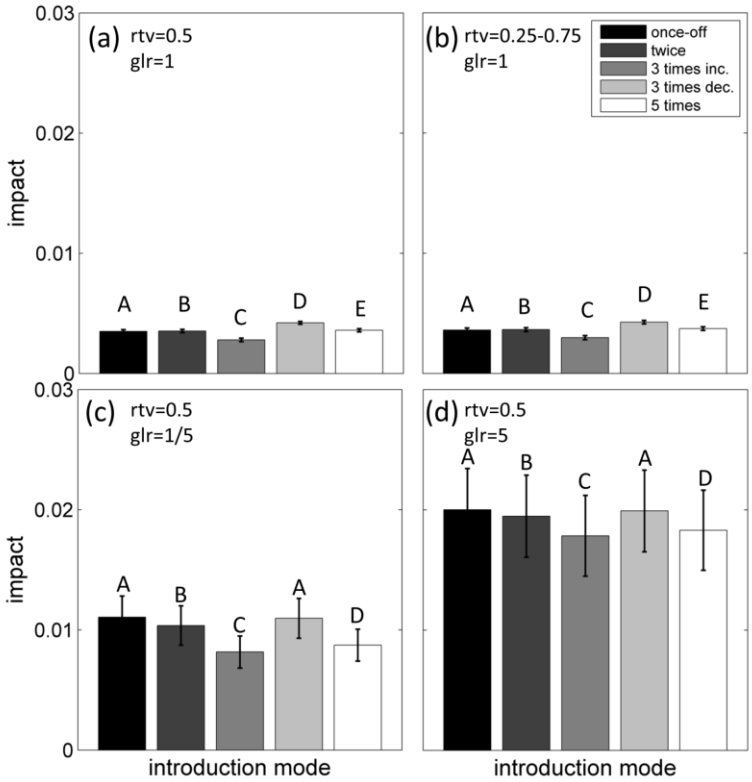

Figure 4: Average (over 100 medium-size networks) of the impact when the alien has: (a) typical trait and similar level of generalization to the native species, (b) average trait and similar level of

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generalization to native species, (c) typical trait and is more specialist than native species, (d) typical trait and is more generalist than native. Error bars represent tenth of the standard deviation. *rtv* stands for relative trait value and *glr* stands for generalization level ratio. Bars with different characters are significantly different from each other.

Role of network structure and stability

Although most network architectural metrics had a significant relationship with network stability metrics (including invasibility), these relationships are quite weak, with the strongest being between modularity and invasibility (Spearman's rank correlation r=0.33; Fig.5). Network connectance is the weakest related to network stability yet still significant with network robustness (r=0.13) and invasibility (r=-0.10), regardless the initial propagule size of the invader (Fig.5, Fig.S5). Specialization and modularity affect all network stability positively (including positively with invasibility). In contrast, nestedness is negatively correlated with most network stability metrics, except for its positive relation with invasion impact (Fig.5, Fig.S5).

Network architectural metrics are more closely related with themselves rather than with metrics of network stability or invasibility. In particular, modularity and specialization are strongly positively correlated (r=0.96), while nestedness forms a hook-shaped relationship with other network architectural metrics. Network stability metrics are also more strongly correlated within themselves rather than with network architectural metrics. Specifically, we noticed strong positive relationships among resilience, invasibility and disruptiveness, regardless of the initial propagule size (Fig.5, Fig.S5). Measurement of invasion impact has the lowest correlations with metrics of network stability (Fig.5, Fig.S5). Of particular interest, although invasibility, disruptiveness, impact and invasiveness are conceptually measures of network instability, they are nonetheless positively correlated with network robustness and resilience. That is, the most robust and resilient community is also the one that is the most disruptive and easy-to-invade, suggesting the existence of two conceptually related but distinct groups in network stability metrics.

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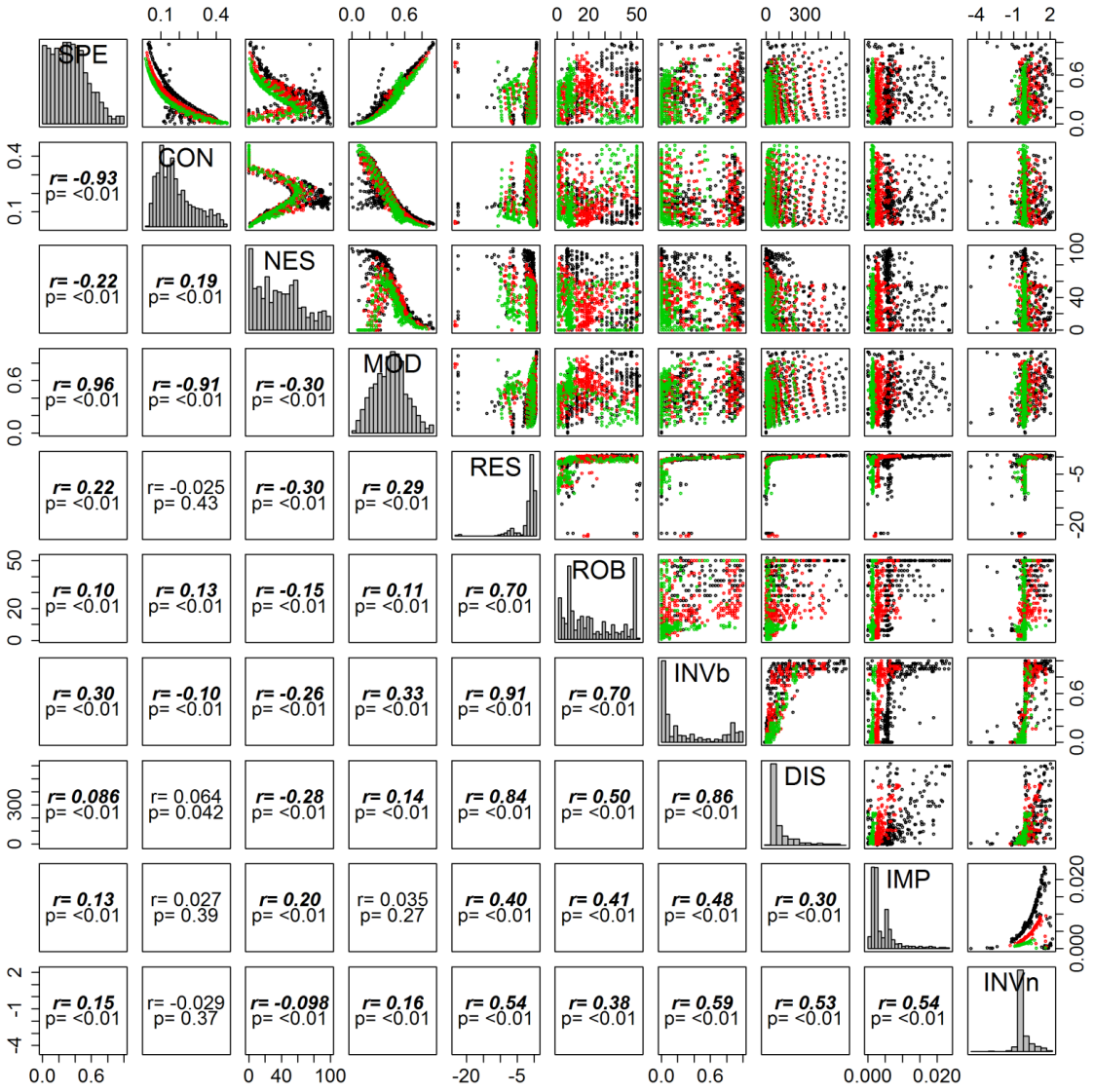

Figure 5: Spearman's rank correlations between network metrics. The lower triangular block gives the rank correlation coefficient (*r*) and the p-values. Diagonal plots represent histograms of each network metric. Green, red and black dots represent respectively small, medium and large size networks.

Using multidimensional scaling analysis, we confirmed that there are two groups of metrics for network architecture and stability (Fig.6). The k-mean clustering analysis gave an optimal number of three clusters, irrespective of the propagule size, with more than 95% variance explained. There is an additional third group containing nestedness, invasion impact and the invasiveness (Fig.6b, 6c). When the initial propagule size of the invader is small (5%

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of the average native density), invasiveness became less related to nestedness but joined the group of network stability metrics (Fig.6a). Results from the hierarchical clustering using a p-value >0.95 confirmed once again about the two groups of network metrics, in agreement with the grouping from the k-mean clustering analysis (Fig.6). Members of the third additional group are either divided into the other two main groups or left in isolation. In particular, nestedness is generally weakly related to both main groups of network metrics (Fig.6a, 6c).

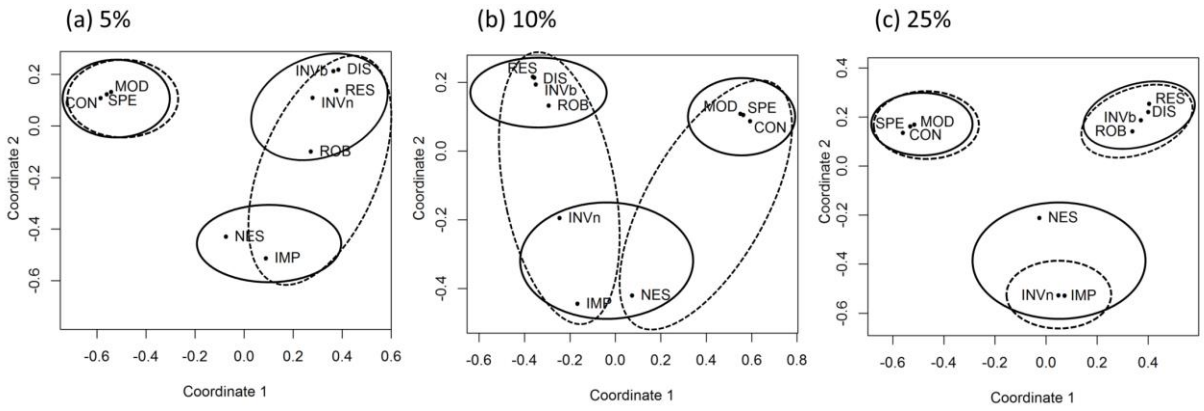

Figure 6: Multi-dimensional scaling representation of the relationship between all network metrics under different propagule sizes, in which respectively (a) 95.5%, (b) 95.2 and (c) 96.3% of the variance was explained. The number of introduced individuals is respectively (a) 5%, (b) 10% and (c) 25% of the average native population densities. Clusters formed by the k-mean clustering analysis are shown by solid circles and those from a hierarchical clustering by dashed circles.

4- Discussion

Trait-mediated invasiveness and impact

Ecological network approach in which interactions are mediated by traits constitutes an interesting framework to predict the success or the failure of an invasion. It allowed us to test the invasion success for different combinations of invader characteristics (trait and level of generalization) and the characteristics of the recipient community. Opposing to previous studies (Aizen et al. 2008; Albrecht et al. 2014; Campbell et al. 2015), we found that the

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effect of invader characteristics on its invasion success is not unidirectional but intertwined. That alien species with traits dissimilar to those of the natives are the most invasive ones is consistent with previous studies (Aizen et al. 2008; Campbell et al. 2014), while the importance of high interaction generalization to invasiveness (Aizen et al. 2008; Bartomeus et al. 2008; Vilà et al. 2009; Albrecht et al. 2014) is only observed when the invader has dissimilar traits from the native. Our results, thus, encompass broader scenarios than those previously studied on mutualistic networks.

The most invasive species is not always the one that has the biggest impact, highlighting the need to differentiate highly invasive species from those with big impact in management prioritization. Not only just scrutinizing trait distinctiveness, a high level of interaction generalization is a strong predictor for big impacts (Aizen et al. 2008; Albrecht et al. 2014), often through the cascading effect of interactions that are strongly associated with generalists. Different from Campbell et al. (2015) but consistent with Morales & Traveset (2009), we found that invaders with traits atypical of the native community have the least impact to native population sizes. Since the overall impact observed in our model is detrimental rather than proliferating (Fig.S1), the impact probably could have resulted from intra-specific competition in mutualistic networks, suggesting that the detrimental effect from competing with invaders has overridden the proliferation from mutualistic interactions. The impact of biological invasions on native population densities is small in mutualistic networks, and thus a negligible effect on network architecture (Fig.S7). Such small impact has been previously documented (Vilà et al. 2009; Padrón et al. 2009) and can be caused by the peripheral role of the invader in the network. In particular, Albrecht et al. (2014) found that the overall number of modules in an empirical pollination network was not altered by invasion, but only that modules were more connected from the super-generalist invaders.

Propagule pressure and introduction mode

Both the number of introductions and the propagule size at each introduction matter to invasion success. Even if the dependence of invasion success on the number of introductions showed contingent patterns on the level of invader generalization, a general pattern still acknowledges the importance of multiple introductions, especially with decreasing propagule size, consistent with previous studies (Jeschke & Strayer 2006; Simberloff 2009). Indeed, a high number of introductions could help in lessening environmental stochasticity (Simberloff 2009) or rescuing the establishment of each introduction as in the phenomenon of invasion

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meltdown (Traveset & Richardson 2014). In our case, this is probably caused by the indirect positive effect of mutualism: once some individuals of the invader establish in the system, they proliferate the population densities of their mutualistic partners and subsequently facilitate the establishment of new arrivals from future introductions, potentially forming a positive feedback between aliens and natives in mutualistic networks (Memott & Waser 2002; Bartomeus et al. 2008; Traveset & Richardson 2014). Moreover, the additional effect of decreasing propagule size in multiple introductions suggests that such proliferation from earlier introductions is diminishing or saturating with the number of established individuals.

Network architecture and invasibility

Network structures, such as connectance, level of specialization, nestedness and modularity, were shown to be not of primary correlates of network stability. Consequently, network architectures alone cannot capture the overall functioning of ecological networks. More importantly, one measure of network stability would suffice for predicting how a community responds to the perturbation of biological invasions. We are certainly not discarding the role of network architectures in stabilizing or destabilizing mutualistic networks (Bastolla et al. 2009; Th*é*bault & Fontaine 2010; Allesina & Tang 2012; Rohr et al. 2014; Vieira & Almeida-Neto 2015), but simply states that inferring network function from structure could have be overemphasized. In particular, nestedness was negatively correlated with resilience and robustness, consistent with previous studies (Allesina & Tang 2012; Campbell et al. 2012), even though it has been observed as one of the most prominent characteristics of mutualistic networks. This counter-intuitive observation is reconciled by our results that highly nested networks have a low invasibility, thus less likely to be invaded.

The more robust and resilient a network is, the more susceptible it is to invasion. Mutualistic networks which are well posed (high robustness) can return quickly to a steady state after perturbations (high resilience); such network features also make it susceptible to invasion (high invasibility; i.e. a high chance of invasion success). That is, networks that are insensitive to perturbations will have a high chance to be invaded. The positive relationships between network stability metrics (resilience and robustness) and network instability metrics (invasibility, invasiveness, disruptiveness and impact) heighten the necessity to use appropriate measures in network studies. Stability metrics should, therefore, not be interpreted outside the context defining environmental drivers of change (Ives & Carpenter 2007). Moreover, network resilience and disruptiveness are strongly related to each other

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(Fig.6). As the former is widely used as a proxy of ecological stability and the latter evolutionary instability, resilient networks are disruptive. Ecological stability and evolutionary stability could be two complementary strategies for systems to handle perturbations.

Future works can expand the scope of our model in two aspects. First, although we were able to vary the interaction generalization level of the invader, the levels of interaction generalization of all native species were assumed to be the same (i.e. the tolerance to trait difference σ_m). This assumption could have oversimplified the reality that species in real networks often have different diet breadths. Second, we assumed a symmetric model regarding the animal-plant interaction. Empirical studies have often unveiled imbalanced roles of animal pollinators and flowering plants in mutualistic networks, resulting in asymmetric interaction with plants strongly dependent on the pollinators (Bascompte et al. 2006; Aizen et al. 2008). Extension of our trait-based model to encompass interaction asymmetry would certainly be worth further investigation.

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Supplementary materials

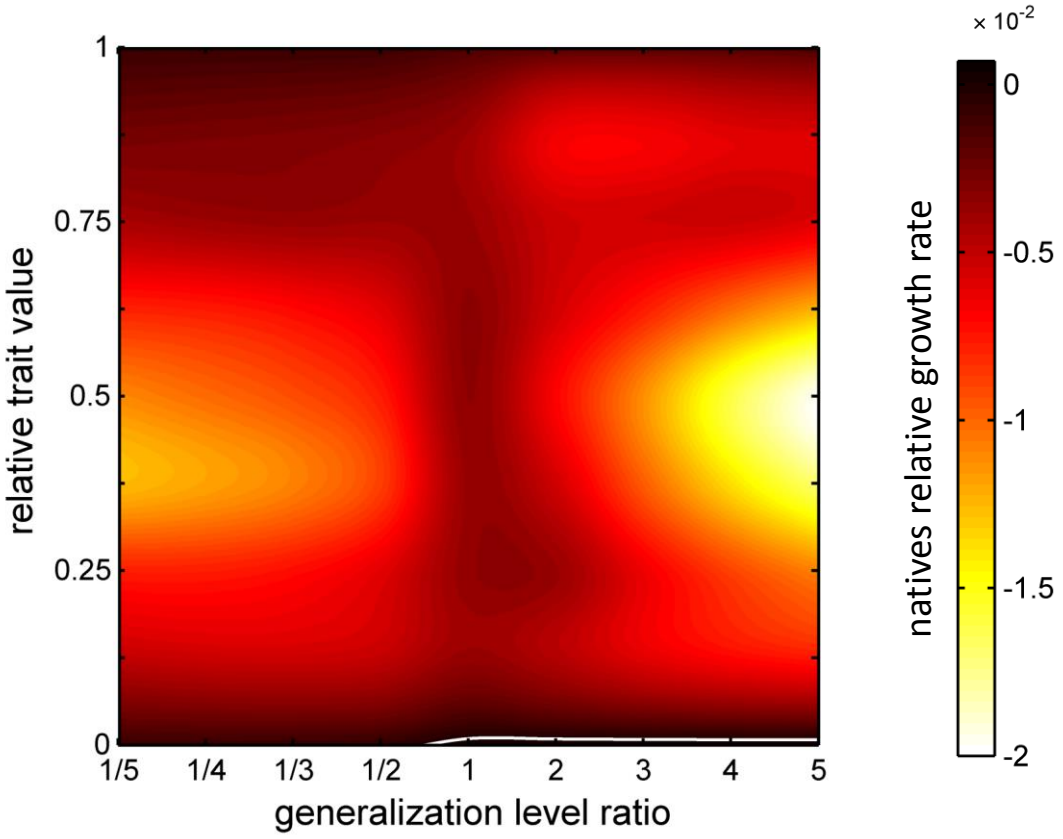

Figure S1: Relative growth rate of the native species (average over 100 medium size networks) as a function of the invader characteristics for once-off introduction. The white line near the bottom right represents the zero growth line.

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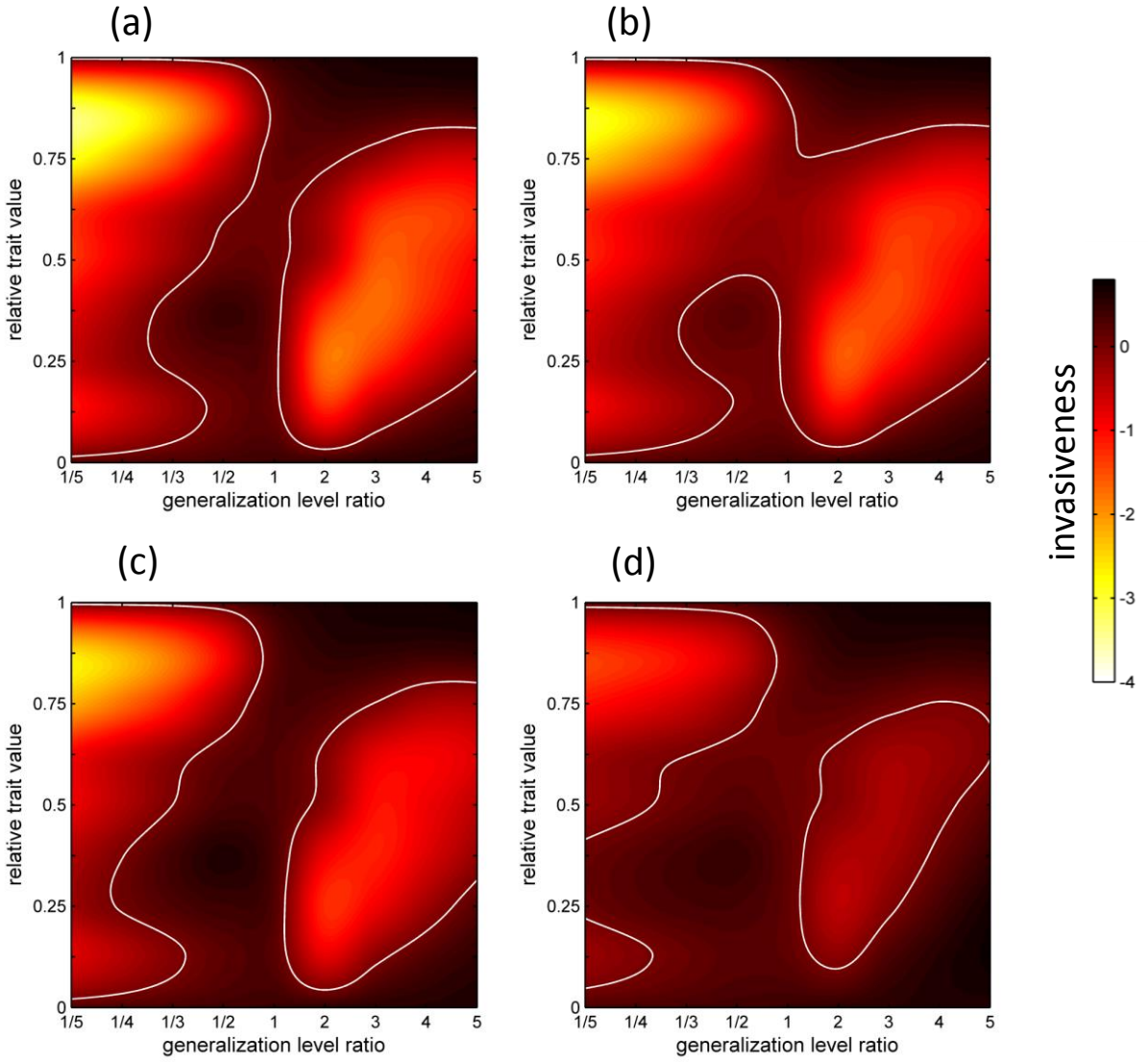

Figure S2: Invasiveness (average over 100 medium size networks) as a function of invader characteristics when introduced (a) twice with equal propagule sizes, (b) three times with increasing propagule sizes, (c) three times with decreasing propagule sizes and (d) five times with equal propagule sizes. White lines represent the zero invasiveness.

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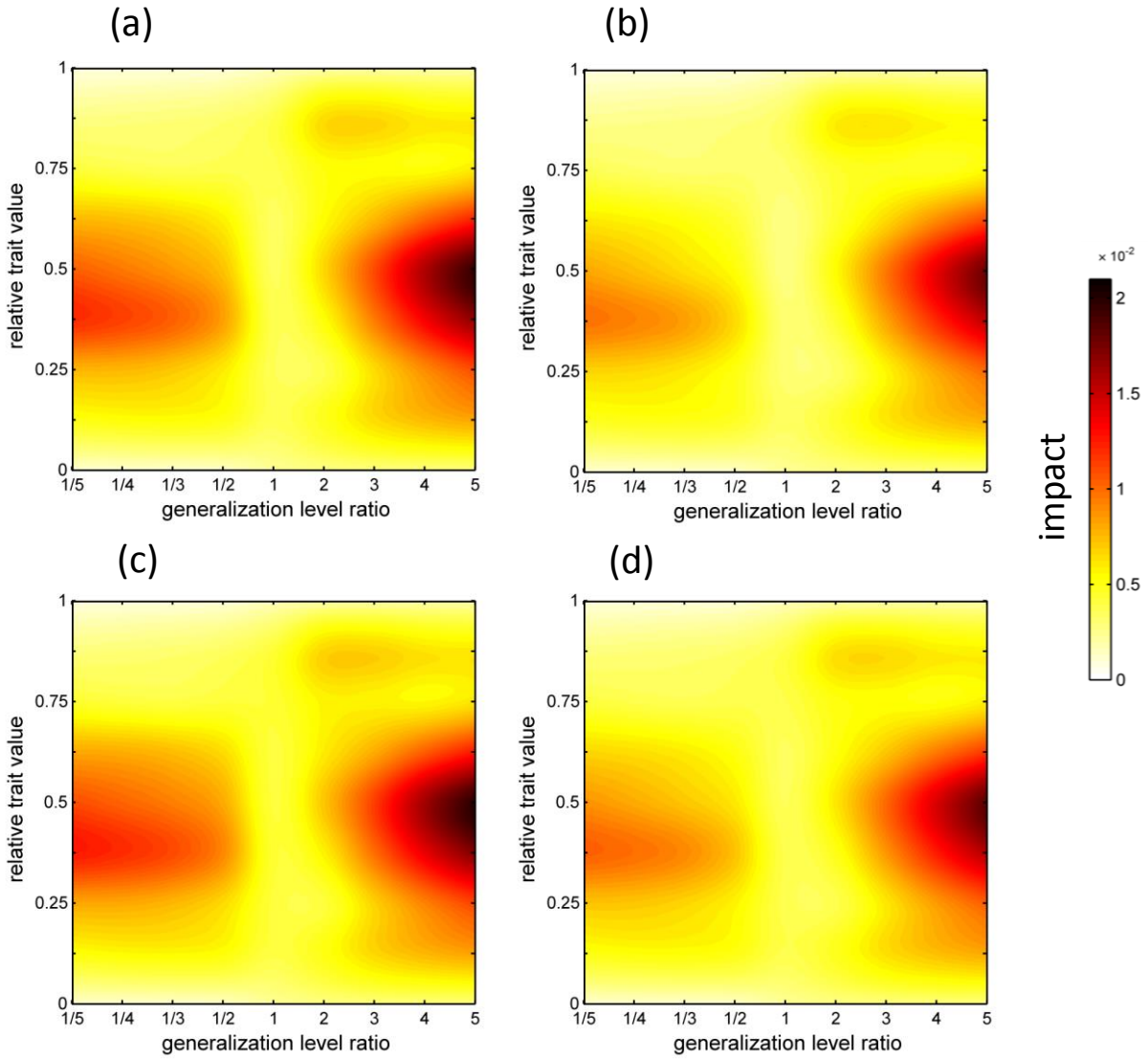

Figure S3: Impact (average over 100 medium size networks) as a function of invader characteristics when introduced (a) twice with equal propagule sizes, (b) three times with increasing propagule sizes, (c) three times with decreasing propagule sizes and (d) five times with equal propagule sizes.

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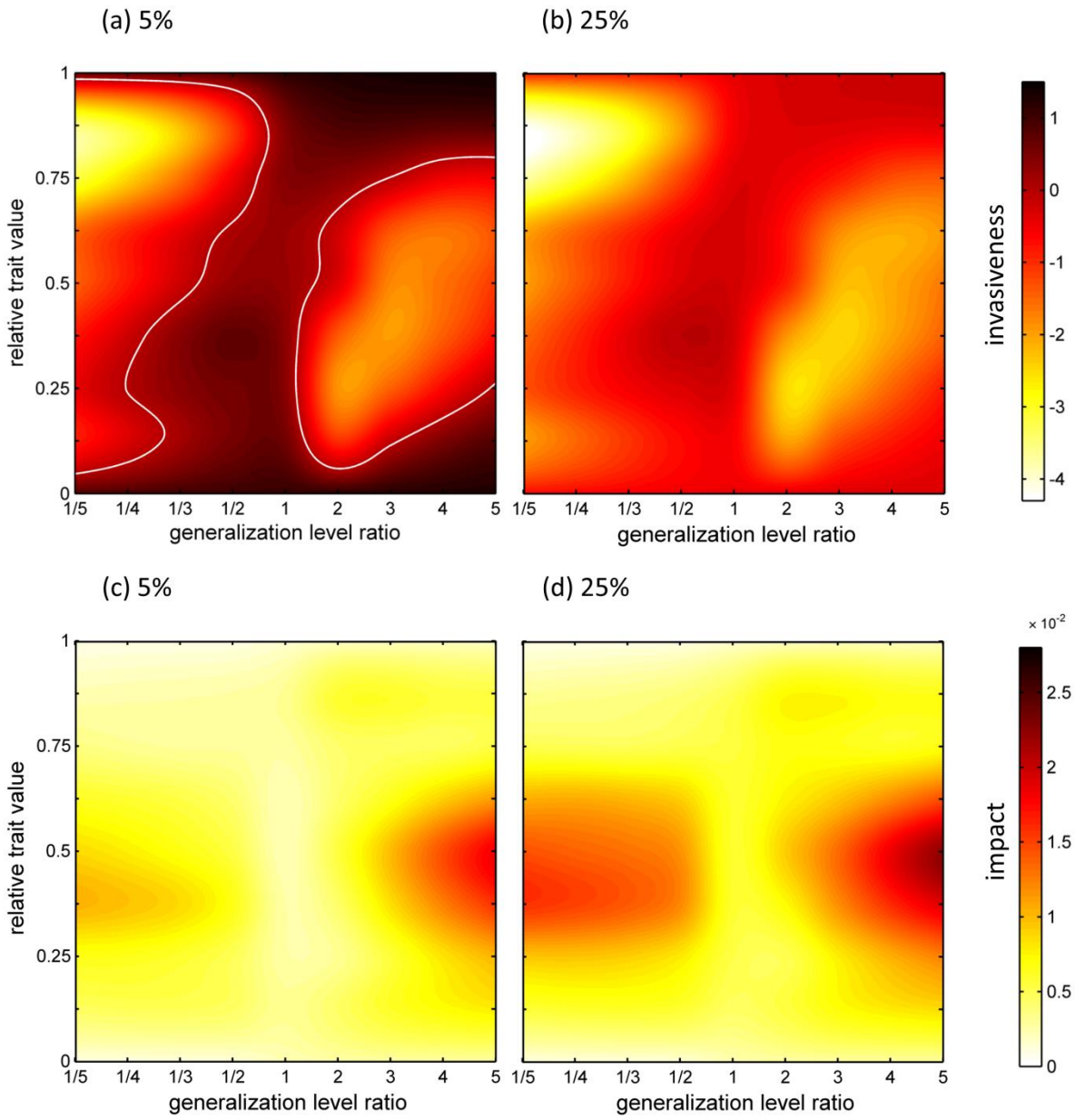

Figure S4: Invasiveness (a, b) and impact (c, d), average over 100 medium size networks, as a function of invader characteristics when introduced once-off, under different initial propagule sizes. (a) and (c): 5% of the average native density; (b) and (d): 25% of the average native density. White line represents the zero invasiveness.

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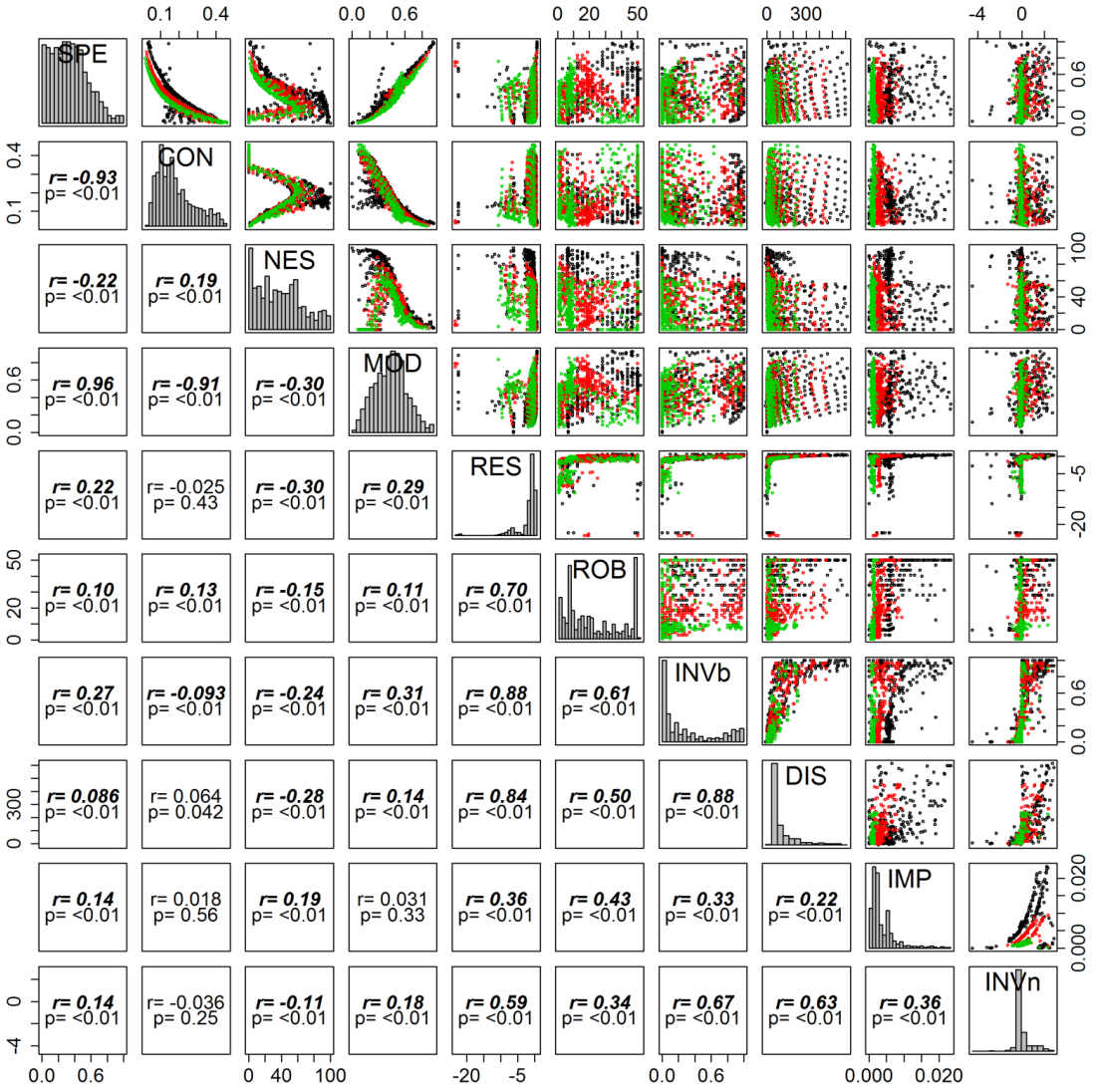
initial propagule size = 5%



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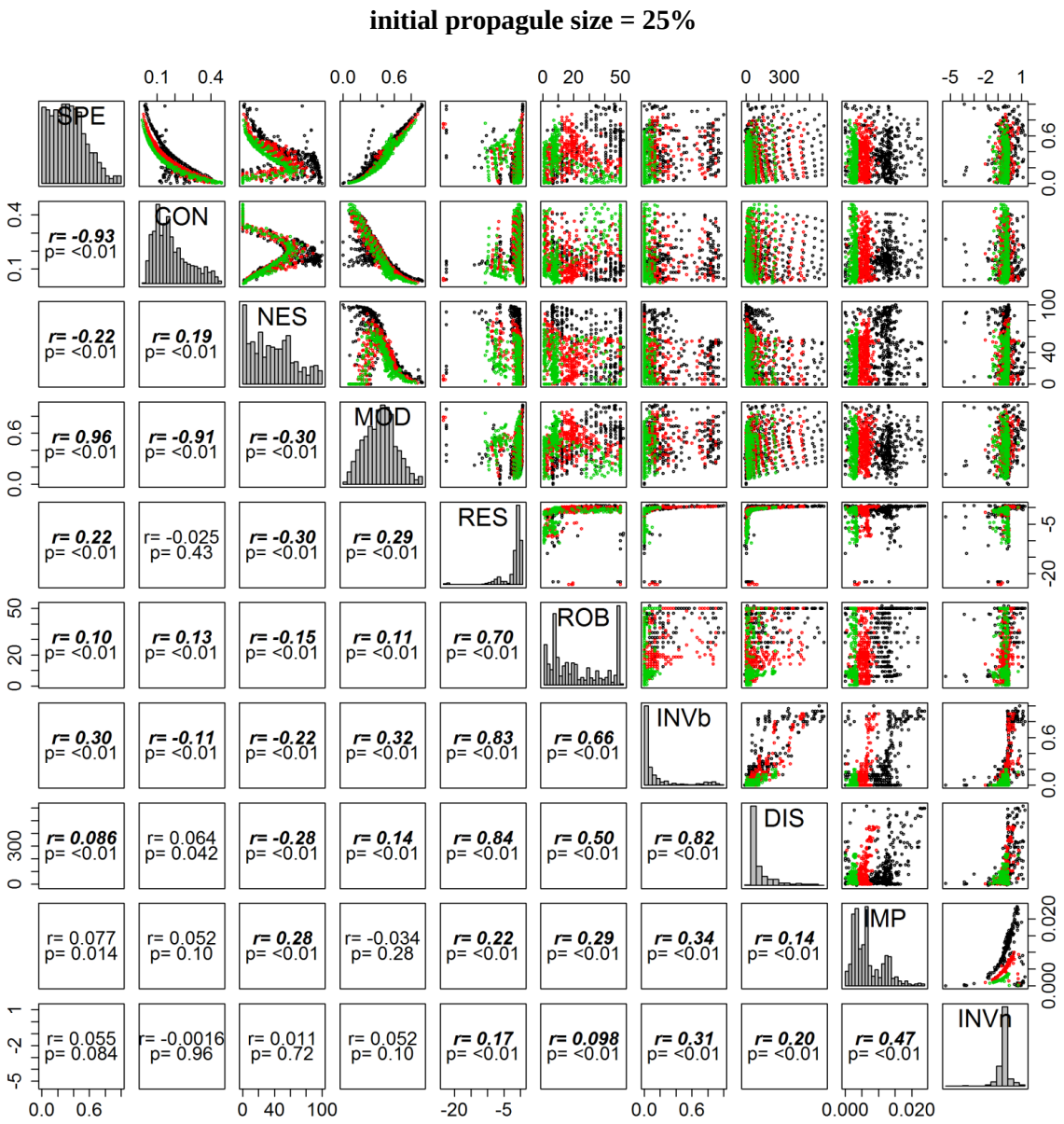

Figure S5: Relationships between all network metrics for different initial propagule sizes. The lower triangular block contains the Spearman's rank correlation coefficient (r) and the p-values. Diagonal plots represent histograms of each network metrics. Green, red and black dots represent respectively small, medium and large size networks.

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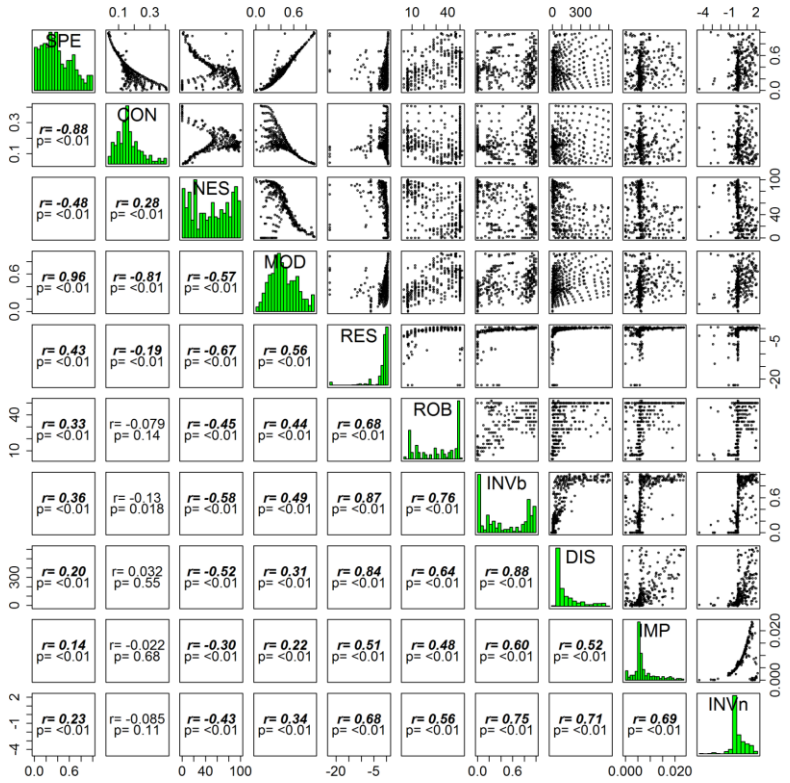
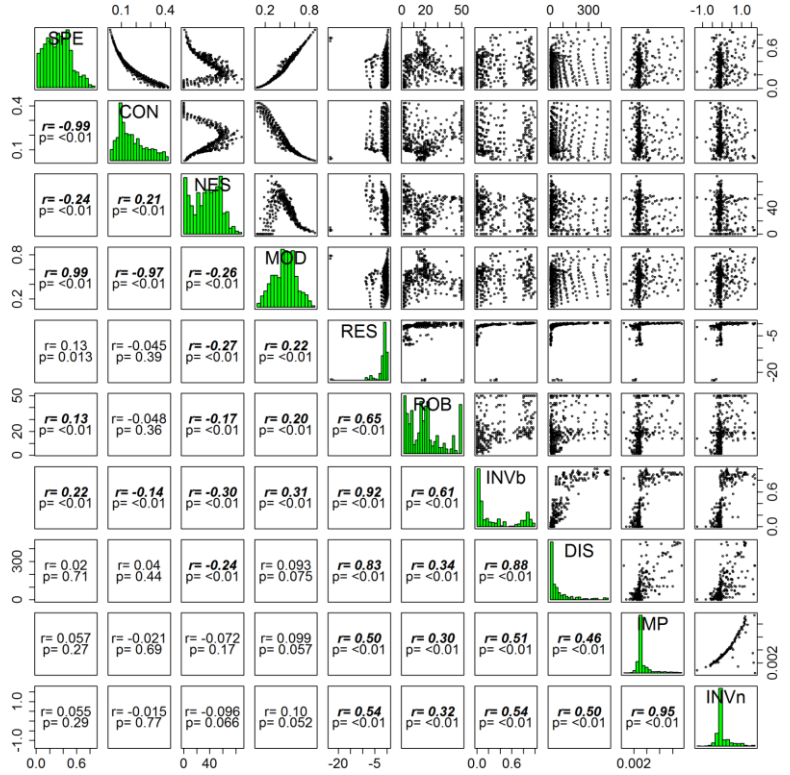
small networks



medium-size networks



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large networks

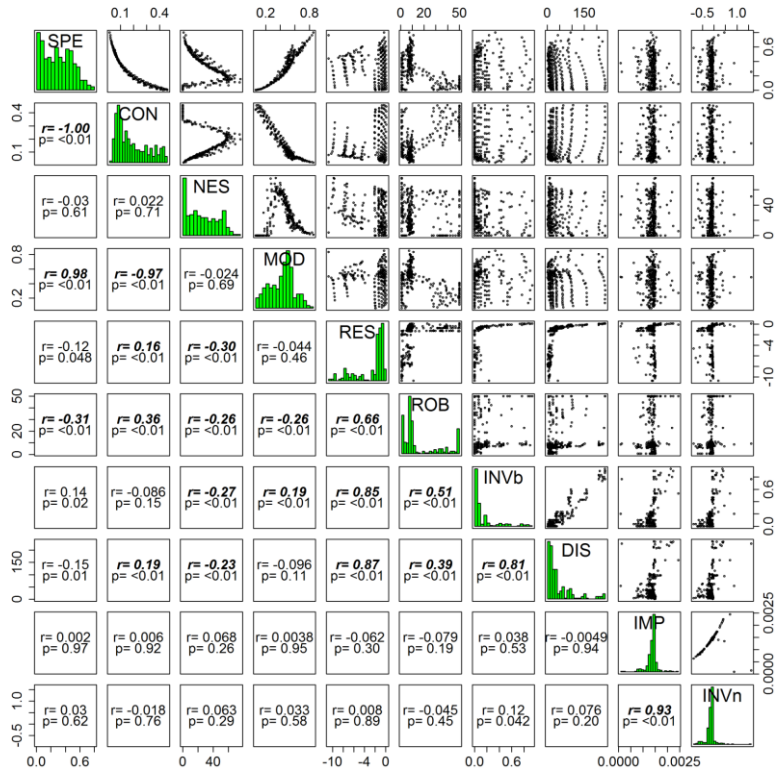

Figure S6: Relationships between all network metrics for different network sizes. The lower triangular block contains the Spearman's rank correlation coefficient (r) and the p-values. Diagonal plots represent histograms of each of the network metrics. Green, red and black dots represent respectively small, medium and large size networks.

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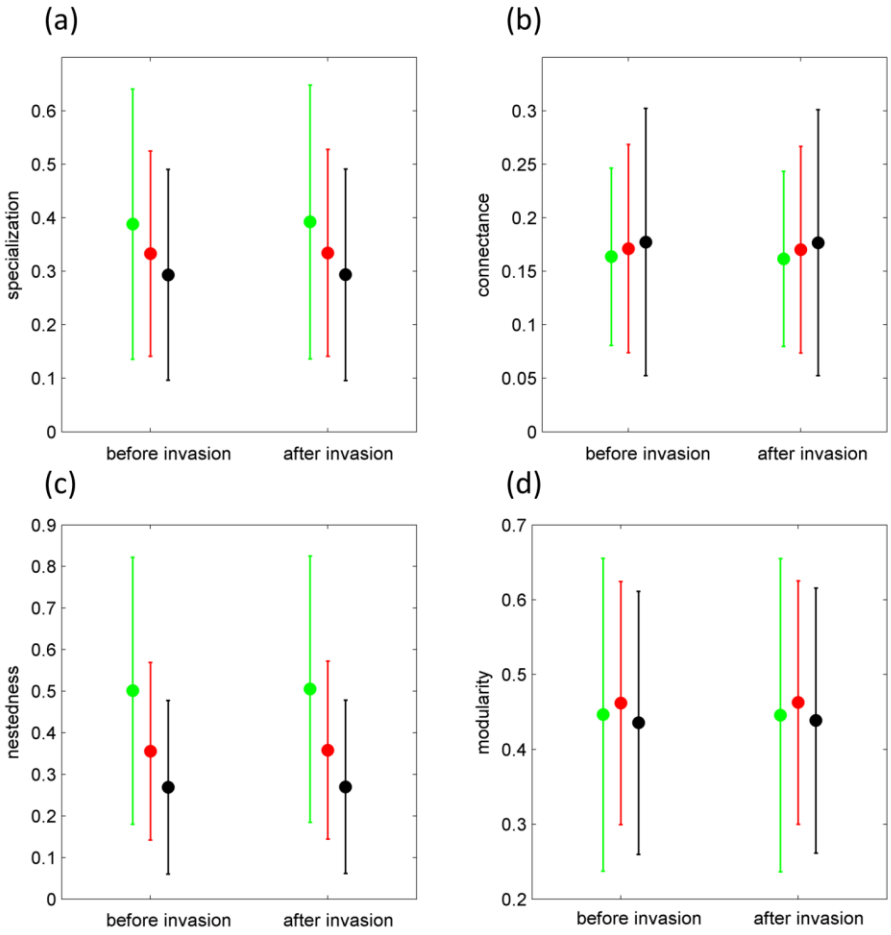

Figure S7: Comparison of network architectures between pre- and post-invasion networks. Points represent the average values over all networks. Error bars are standard deviations. Green, red and black colours represent respectively small, medium and large size networks.

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CHAPTER 6

Conclusion

"Struggle is pursuit of advantage; once emptiness and fullness are determined, one may then struggle with others for advantage."

Li Quan, In *The Art of War*

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Summary

By coupling the ecological dynamics of population densities and the evolutionary dynamics of functional traits, we uncovered important ecological and evolutionary processes responsible for the emergence, the maintenance and the stability of mutualistic communities. Starting from a mutualistically interacting ancestral pair of animal morphospecies and a plant morphospecies, we allowed the morphospecies to co-evolve adaptively under rare mutations and frequency-dependent selection. Morphs could undergo either directional selection or an adaptive diversification leading to the emergence of multiple interacting morphs. Hence, we were able to build complex adaptive networks of mutualistic interactions.

Since species in a community are simultaneously under different selection pressures (such as those from predation and intra-trophic competition), we showed that mutualism is only a weak disruptive force whereas a strong frequency-dependent intra-trophic competition is the main driver of adaptive diversification, leading to polymorphism. Hence, mutualism enhances evolutionary stability of the community. Nevertheless, it plays an important role in maintaining high population densities and the overall productivity of the community.

Moreover, these selection pressures may often be opposing each other, resulting into the presence of bistability and bifurcation in the eco-evolutionary trajectories of the community: the system chooses to prioritize either resource exploitation or mutualistic support especially when mutualistic interactions are specialized. Interestingly, with perturbations, eco-evolutionary trajectories converge into a unique scenario in which mutualism creates empty niches favourable for invasion in specialized mutualistic networks. Evolutionary response of the community facing invasion is often manifested by a strong directional selection.

Furthermore, we were able to generate mutualistic networks with characteristics comparable to empirical networks by using our model. By doing so, we showed the importance of trait-mediated interactions in explaining the well-known asymmetric structures of mutualistic networks. Three network assembly forces were detected to be crucial in generating these structures: resource accessibility, tolerance to trait difference between mutualistic pairs and competition.

Finally, we used these modelled networks to explore the ecological response of mutualistic networks to biological invasion. We were then able to determine characteristics of an introduced species that can promote its invasiveness: its trait should differ from those of the

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native species and its level of interaction specialization should be similar to that of the native community average. The invasion should even be more successful if aliens are introduced several times with declining propagule sizes. Surprisingly, the most successful invader is not always the one that has the biggest impact. Furthermore, the invasibility of the recipient community does not primarily depend on its structure. Other measurements of network stability such as robustness, resilience and disruptiveness are better predictors of invasibility.

Hence, this thesis has shown that modelling the interdependence of ecological and evolutionary mechanisms can be an interesting approach to tackle important ecological and evolutionary questions raised in the study of mutualistic networks. These questions can range from explaining the pattern of emergence of biodiversity and network structure, to identifying factors responsible for both ecological and evolutionary stability of mutualistic networks in the face of perturbations such as biological invasion.

Caveats and future directions

Although based on reasonable assumptions, our approach was purely theoretical and its importance lies in its predictive power. However, the use of empirical datasets to test our model would be encouraged for future research. For instance, one can consider a set of empirically measured trait values as well as population densities of all the species involved in a specific mutualistic network. From the knowledge of these empirical values, one can use our model to infer the possible interaction specialization or the competition strength that could have resulted into the emergence of the empirical network. This will give an idea of the main assembly forces responsible for the structure of the network. Moreover, if time series datasets of trait values and population densities are available, our model can be used to simulate an approximation of the eco-evolutionary trajectories of the community and predict its response to biological invasion. It is however important to notice the scarcity of time series datasets as they usually require sampling over a long time period for several generations.

The model permitted us to unveil the response of mutualistic networks to biological invasion. However, biological invasion only represents one specific aspect of environmental perturbations faced by mutualistic communities. It would also be interesting to use our approach to explore other aspect of environmental perturbations such as climate change or habitat destruction. In the latter case, mutualistic networks will be allowed to evolve not only

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through time but also through space. This will add one more dimension to the model. Although not trivial, this extension can be of great interest.

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"Because from Him, and through Him, and for Him, are all things. To Him is the glory into the ages. Truly."

Romans 11:36

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